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REPRODUCTIVE STRUCTURES AND EVOLUTION IN *LUDWIGIA* (ONAGRACEAE). III. VASCULATURE, NECTARIES, CONCLUSIONS¹

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ABSTRACT

To complete this survey of floral structure the number of *Ludwigia* species prepared anatomically—cleared, sectioned, or both—was increased to 37. In general, nectaries of diplostemonous ludwigias are trichome-covered depressions in the (often raised) summit of the ovary, whereas nectaries of sects. *Dantia*, *Microcarpium*, and *Miquelia* are convex and hairless. Nectaries of sect. *Ludwigia*, though hairless, are otherwise closer to those of the diplostemonous ludwigias. Vascular features are not useful for grouping *Ludwigia* species. For example: the degree to which petal midveins extend basally differs markedly from species to species, some midveins ending in the vascular girdle, others passing through the girdle to the flower's base. But species that are alike for this trait are too unlike in others ways to be allied. The level at which the major bundles of a *Ludwigia* flower part is not a trustworthy indicator of evolutionary level: in some species, at least, it has more to do with the shape of the flower than with gradual phyletic union of appendages. In some ludwigias large bundles in the locular radii retard dehiscence and ensure slow dispersal of seeds. Onagraceous styles commonly carry one bundle in each locular radius and no others, but some of the ludwigias have a second set in the septal radii at the style's base, apparently an archaic trait. *Ludwigia* is the only onagraceous genus in which ovules are supplied by central as well as by transseptal bundles, a peculiarity linked functionally with deeply intrusive placentas and maybe with pollen tetrads. To account for this dual supply—at the same time for *Ludwigia*'s oddly placed nectaries and lack of a floral tube—I argue that epigyny evolved twice in the family, once in the line leading to *Ludwigia* and once in the line leading to all other onagrad.

Gynoecial nectaries and a central ovular supply are among the traits that set *Ludwigia* apart from other onagraceous genera. Throughout the family vascular bundles supplying the ovules pass transversely through the septa of the inferior ovary. *Ludwigia* species commonly have additional bundles running up the center of the ovary. The central system is reported here for the first time along with other aspects of floral vasculature deemed to have systematic worth. I shall argue

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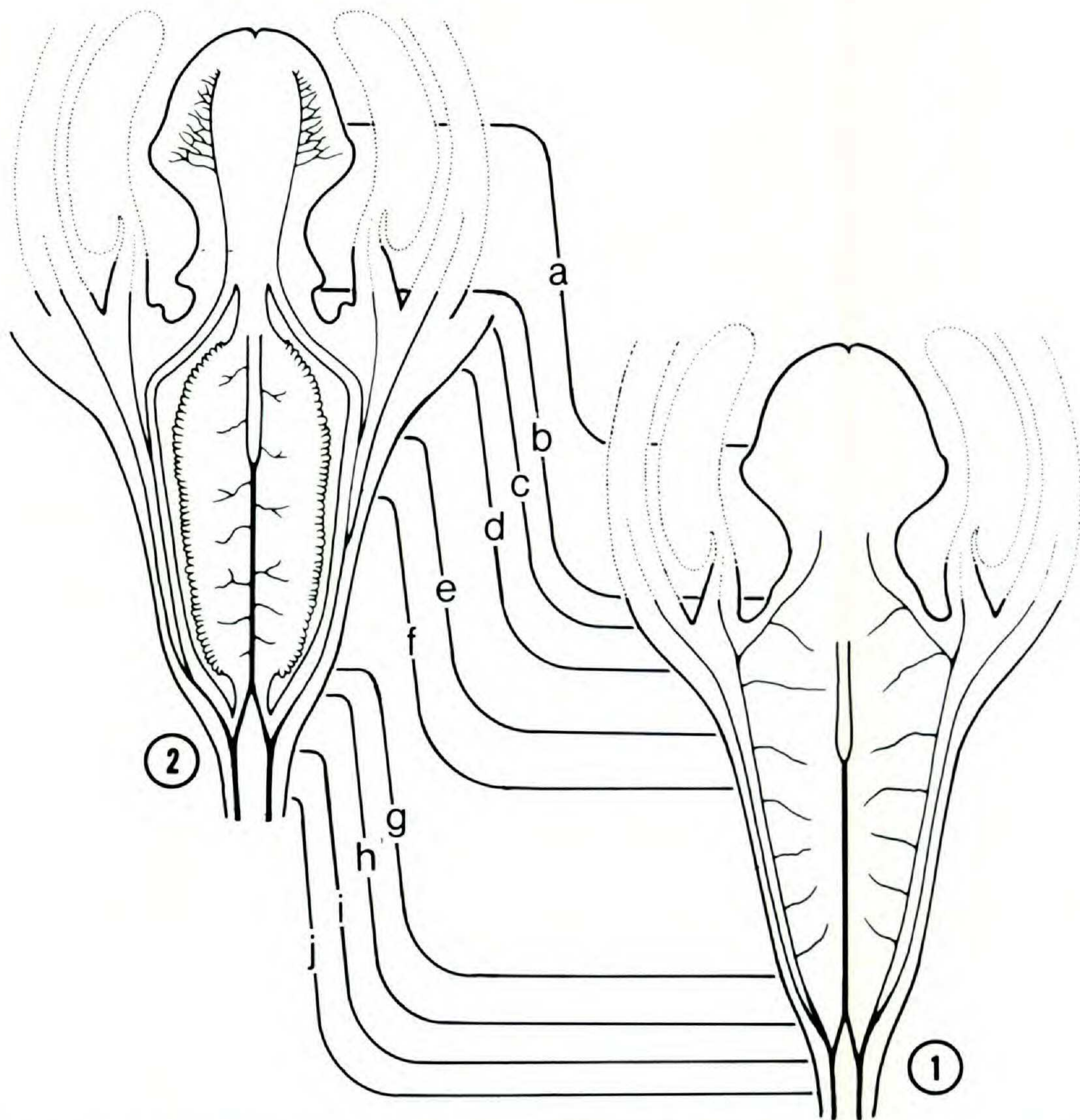
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that this system stems from preonagraceous ancestors, offer a concordant explanation for the gynoeceal nectaries, and sum up what we can thereby infer about the evolution of the genus.

As far as I know, no one else has looked closely at the floral vascular bundles of *Ludwigia*. Baehni & Bonner (1949: 357) tried to do so but failed for want of good specimens. Saunders's notorious *Floral Morphology* has a short paragraph on *L. palustris* but the observations are superficial. On the other hand, a number of researchers have looked at floral vasculature elsewhere in the family and have described or figured the characteristic transseptal strands (Duchartre, 1842; Van Tieghem, 1868; Barcianu, 1874; Stadler, 1886; Geerts, 1909; Bonner, 1948; Baehni & Bonner, 1948; Kowalewicz, 1956; Eyde & Morgan, 1973; Orchard, 1975). The appearance of onagraceous nectaries is also well known and an occasional observer has noted the odd form and position of *Ludwigia*'s nectaries with respect to the others (e.g., Feldhofen, 1933: 564). I do not know that any student of the family has heretofore offered an evolutionary explanation for the oddity unless we count Broekens (1924: 447), who mentioned "Diskusbildung" as one of his reasons for deriving Onagraceae from *Trapa* via *Ludwigia* ("Jussieua"). My earlier notion that the gynoeceal nectaries of *Ludwigia* are like the interstaminal nectaries of *Lopezia* (Eyde & Morgan, 1973) now seems farfetched, and I have dropped it in favor of the view presented here.

Vouchers for my serially sectioned flowers were tabulated in the first article of this series (Eyde, 1977), where I grouped them into the subgeneric sections then accepted. An updated version of the table would redistribute the species listed under sect. *Myrtocarpus* to accord with Ramamoorthy's (1979) views, and it would include the voucher for another wet collection—*Ludwigia ovalis* Miq., Boufford 19961 (MO), Japan, sect. *Miquelia*—as well as the additional herbarium specimens cited later in this article. The collections used for sectioning also provided flowers for clearing, some of them cleared whole, some cut beforehand with a razor blade to yield a better view of one part of the vascular system or another. S. Yankowski, who did the technical work for this article and its predecessors, gets good clearings with the following sequence: 5% NaOH, H₂O, Stockwell's bleach (Schmid, 1977), H₂O, chloral hydrate, H₂O, graded ethanol series, xylene. If the flowers have been taken from the herbarium, they are pre-treated with Contrad 70 (Schmid & Turner, 1977) and rinsed with H₂O before they are treated with NaOH. Yankowski examines the material often and varies the timing of each step according to the visible progress of the clearing process. The cleared flowers can be kept indefinitely in covered dishes of xylene, though the fluid must be replenished or changed periodically. We use size zero or 00 artists' brushes to manipulate the cleared flowers when examining them microscopically, and we wear the Mine Safety Appliance Company's Comfo II respirator to avoid breathing toxic xylene vapor. To avoid xylene vapor when cover-slipping sectioned flowers we mount the coverslips in a portable plexiglass hood with an exhaust attachment (Sanders, 1972: 20–21).

The descriptive comments that follow are based more on sections in some instances, more on clearings in others, depending on the quality of the preparations. Two closely approximated bundles, it should be noted, can seem separate to a greater degree in cleared preparations than in sections. The reason for this



FIGURES 1-2. Diagrammatic sections through 4-merous flower of *Ludwigia peruviana*.—1. Septal plane.—2. Locular midplane. Letters mark levels of cross-sections in Fig. 3. Roughly $\times 6$.

is that the eye follows longitudinal sequences of thick-walled xylem elements when clearings are examined rather than the mixture of xylem, phloem, and associated cells followed in sections. Usually bundles containing few thick-walled elements are more plainly seen in sections than in clearings. I paid no attention to the orientation of the floral vascular bundles, that is, to the relative position of xylem and phloem. Not only is it difficult to identify phloem in some material, but I would expect its position to be uncommonly variable in the Myrtales, where internal phloem is of regular, perhaps universal, occurrence.

Floral vascular systems are often described as if the component bundles must develop acropetally. It is now known, however, that some floral bundles originate in isolation and subsequently extend their proximal ends to previously formed bundles (Lawalrée, 1948; Eyde, 1975; Aziz, 1978). This ontogenetic sequence— isolation first, connection later—can be changed phyletically in ways that would be unlikely or impossible if the bundles extended only acropetally. Accordingly, I have tried to write the descriptive passages without an acropetal bias. My reason for doing so will become clearer when I discuss the petal supply in sects. *Ama-*

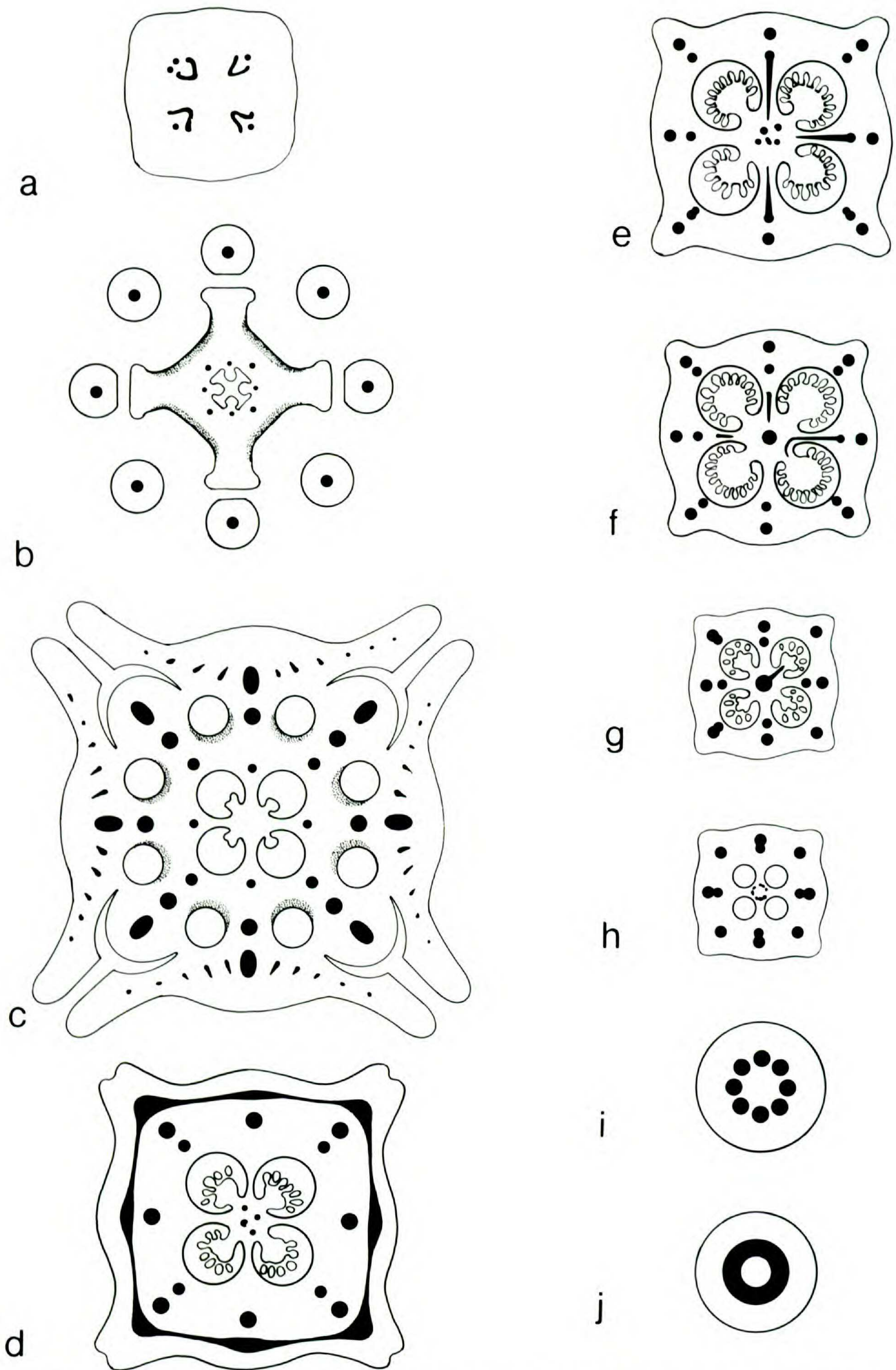


FIGURE 3. Diagrammatic sections through 4-merous flower of *Ludwigia peruviana*. Cf. Figs. 1, 2, and 4. Roughly $\times 9$.

zonia, *Oligospermum*, and *Seminuda*. The flower of *Ludwigia peruviana* is first because I have a sizeable collection on which to base vascular diagrams (Figs. 1–3) and because it is among the more primitive with respect to floral structure. Flowers of this species can be 4-merous or 5-merous; I chose 4-mery to simplify the diagrams.

LUDWIGIA PERUVIANA

The most conspicuous bundles in the flower are the sepal midveins. Followed basally they continue through the wall of the inferior ovary in the septal radii, the course of each marked by a broad external rib that can be visible to the unaided eye. Interior to each sepal bundle and in the same radius is a bundle supplying an antesealous stamen. The paired bundles are close together at all levels (Fig. 1), but they unite only at or below the lowermost level of the locules (see pairs still evident in Fig. 3h).

Petal midveins of this species can also be followed downward into the ovary wall. Each lies in the midplane of a locule accompanied by a bundle supplying an antepetalous stamen. The level at which the stamen bundle joins the basal extension of the petal bundle varies even within the same flower. In my material the junction is always in the lower half of the inferior ovary (Figs. 2, 3g) and in some instances paired structure is evident down to a level below the placentas. This is true only of *L. peruviana*; the junction is at least somewhat higher in all other ludwigias that I have looked at.

At the flower's base, all longitudinal bundles merge in a circle of eight bundles (Fig. 3i)—ten if the flower is 5-merous. Followed deeper into the peduncle the circle becomes a continuous vascular cylinder (Fig. 3j): the level at which this change occurs is probably age-dependent. In some *Ludwigia* peduncles strands consisting only of phloem run through the pith. I have seen such strands in peduncles of *L. decurrens* and *L. pilosa* but not in *L. peruviana*. Similar medullary phloem strands have been found in *Ludwigia* stems (Fukuda, 1967: 352).

All *Ludwigia* species commonly have a pair of bracts below the flower or adnate to the inferior ovary. As monographers have noted, the position of the bracts varies within species and between species, though some species always have higher bracts than others. In *L. peruviana* the bracts (not shown in my figures) usually diverge from the peduncle. Their midveins merge with the peduncle's vascular cylinder in the septal plane, that is, in line with the sepal midvein. In species with higher bracts the median bundles of the bracts may join the sepal supply at or above the base of the flower.

Cross-sections cut slightly below the divergence of sepals and petals pass through a vascular girdle whose segments link the sepal supply transversely with the petal supply. For clarity my diagram (Fig. 3d) shows the whole girdle as if its segments were straight. Actually the segments are somewhat irregular arcs; so a microtome section thin enough to be useful commonly picks up only bits and pieces (but see Fig. 7). To examine the entire girdle one should clear thick free-hand sections, as Sporne (1977) did for his article on vascular girdles. Sporne found girdling bundles in 20 families of dicotyledons, including Onagraceae, where I have found few species to be without them. All *Ludwigia* species have a girdle and it is usually conspicuous; indeed, it is the only vascular feature of

Ludwigia that Baehni & Bonner (1949) could discern. The most prominent parts of the onagraceous girdle are the bundle junctions in the locular radii. In *L. peruviana* and some of the other ludwigias one finds in each such radius a vascular plexus where the petal midvein and the girdle join with the most lateral of the sepal bundles (Fig. 8), in other words, with the outermost subsidiary bundles that run through the sepal more or less parallel to its midvein. Some of the other subsidiary bundles of the sepal—and there may be a dozen or more altogether—join the girdle segments at points between the sepal supply and the petal supply, as in *Epilobium angustifolium* L. and a number of other dicotyledons (Sporne, 1977). Minor longitudinal bundles of the petal do not connect directly with the girdle but merge with the midvein in or above the petal's narrow base.

The short style is supplied by four or five major bundles, depending on the flower's merism, these alternating with four or five minor bundles (Fig. 3b). The major bundles can be identified as carpel midveins by their alignment with the locules. Each ends freely high in the stigmatic region after supplying a featherlike network of fine bundles (Figs. 2, 3a, 4). Basally each major style bundle joins the stamen bundle in the same radius, the junction occurring (in *Ludwigia peruviana*) a short distance below the girdle (Figs. 2, 3e). The minor style bundles end distally below the stigma, and their bases join the bundles supplying the antesealous stamens, the junction occurring just above the girdle.

For simplicity's sake Fig. 1 indicates but a few of the transverse strands that ordinarily pass through the septa of *Ludwigia peruviana*. Ovules number more than 300 per locule in this species, and the transseptal bundles supplying them are plentiful enough that two or three can be seen in most cross-sections. Figures 3e and 3f are idealized in that transseptal bundles seldom if ever run straight through a real cross-section of *L. peruviana*. The upper ones tend to slant downward toward the floral axis, the lower ones upward. Their outer ends join with the antesealous supply except in the top of the ovary, where a few transseptal bundles connect with the minor style bundles.

In addition to the transseptal supply, the placentas receive bundles from a central system that connects below the locules with the flower's main bundles (Figs. 1–2, 3h). The upper half of this system is a somewhat anastomosing group of bundles having no constant position with respect to locules and septa (Figs. 3d–e). Followed downward these converge in a central column from which fine strands supply the placentas (Figs. 3f–g). Basal connections are with all eight or ten outer bundles, and the strands connecting the central system with the sepal supply seem heavier than those linking it with the petal supply.

On the summit of the ovary of *Ludwigia peruviana* there are four or five nectaries aligned with the petals and the locules. Each is a depression shaped like an inverted and somewhat rounded V (Eyde, 1978: fig. 8) with its arms embracing an antepetalous stamen. Evaporation of nectar is retarded by the many stiff trichomes that emerge all around the margin of the depression and jut out over it to form a sort of thatched roof. Delpino observed as early as 1873 that the trichome cover can bar ants and other small robbers but not a bee's proboscis. Figure 3c shows the nectary as two cavities because the cross-section passes through the arms of the V's (nectariferous tissue stippled); Fig. 3b, passing through the tops of the nectaries, shows each as one concavity. Similar nectaries

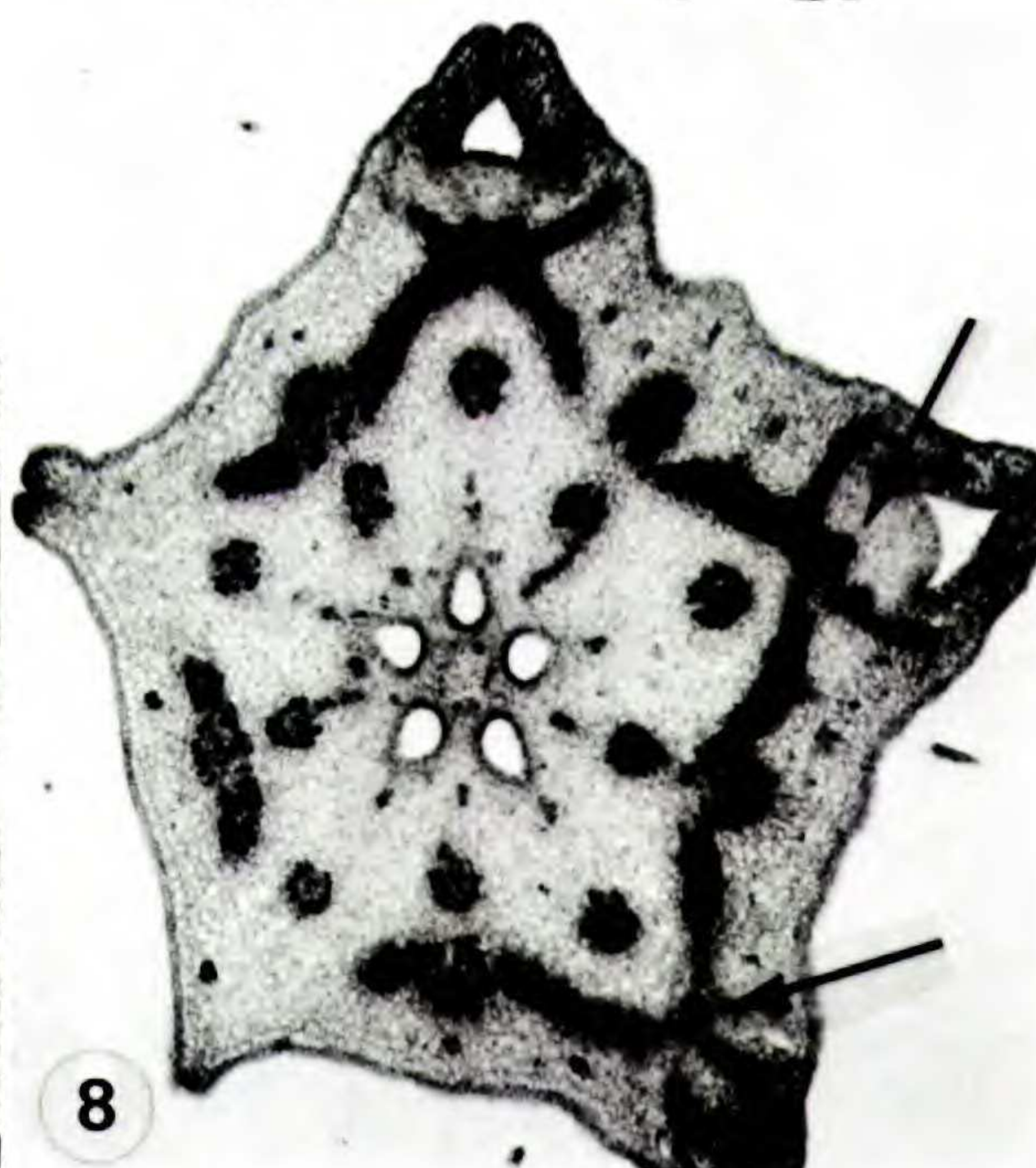
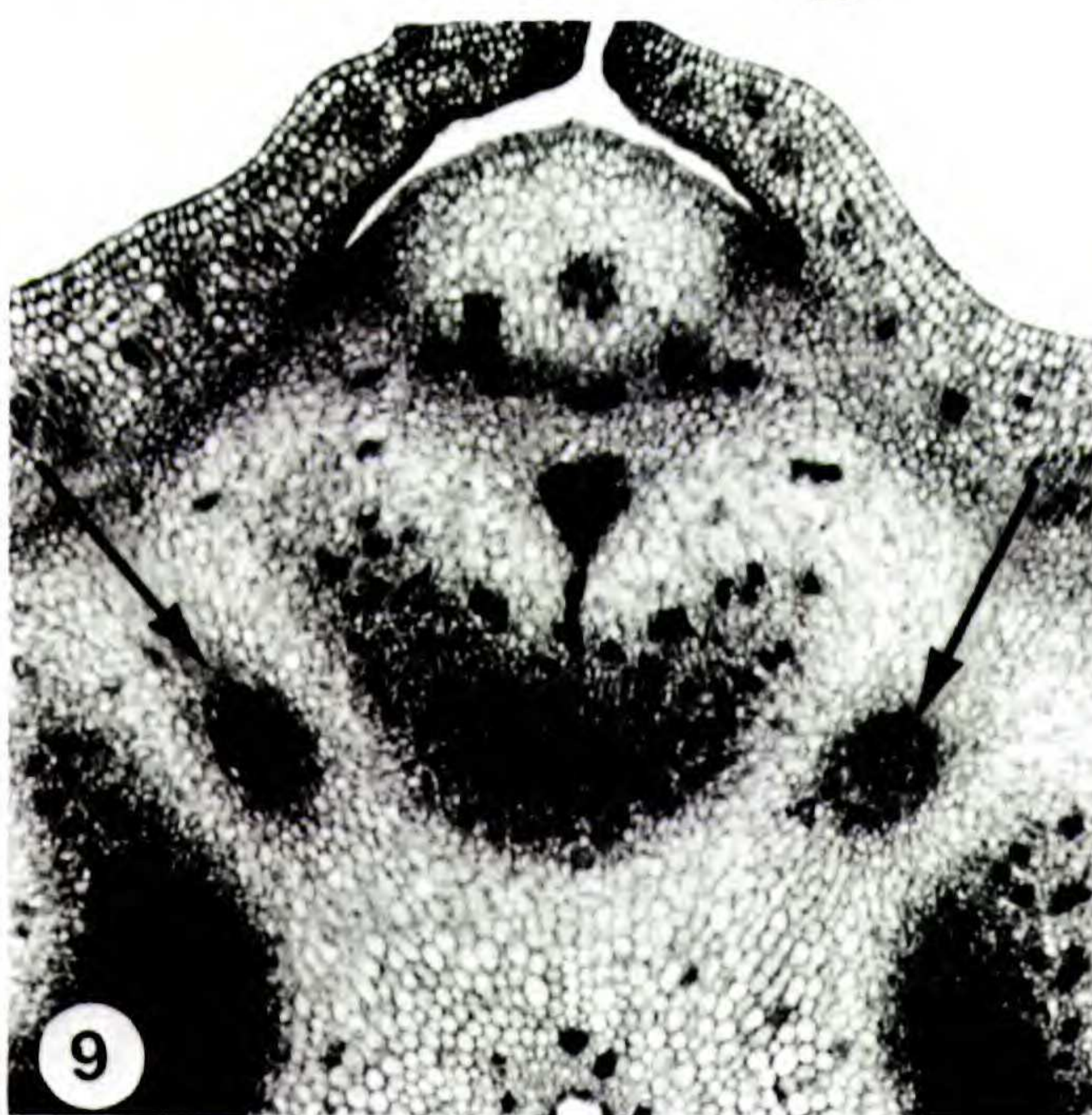
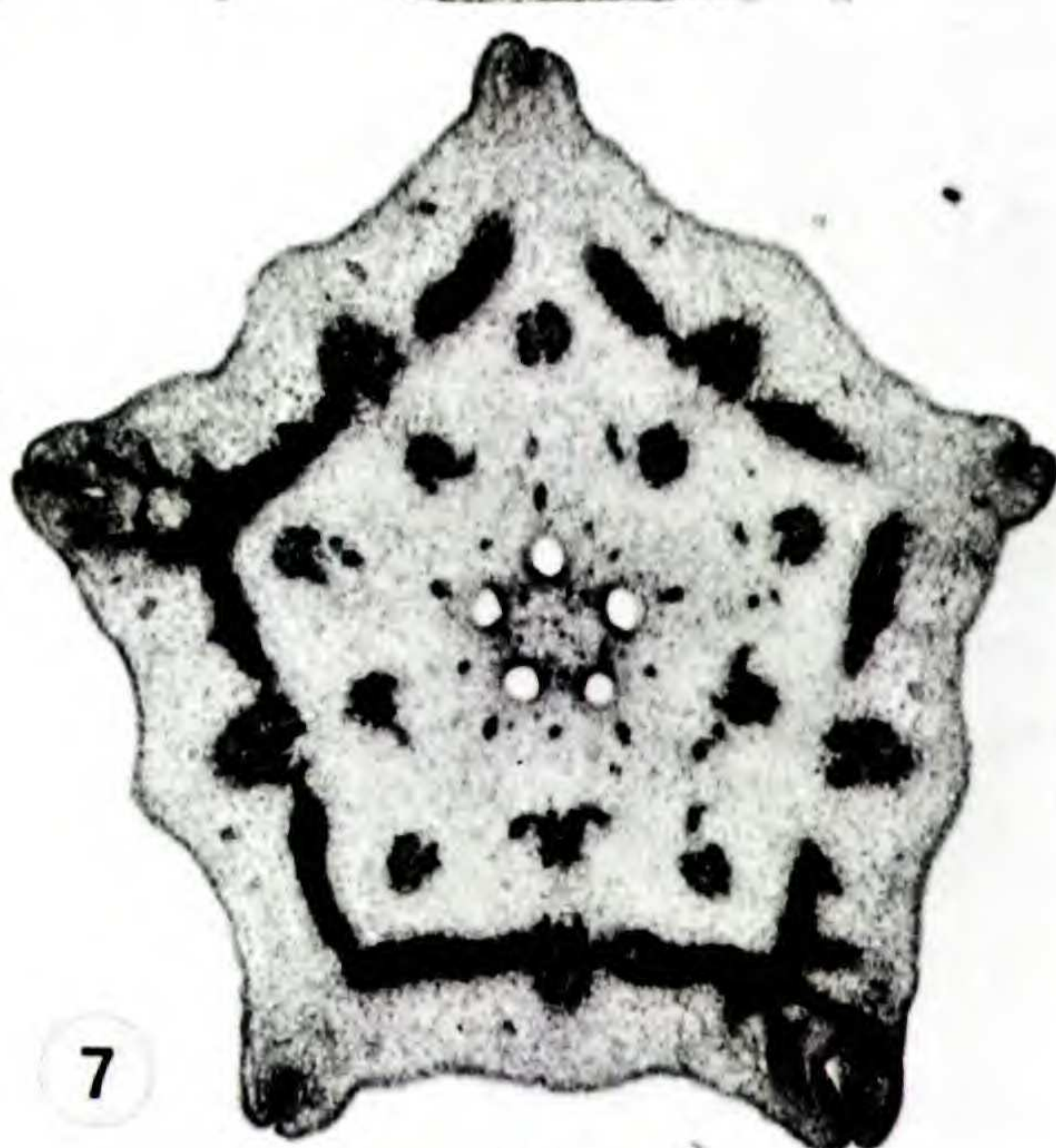
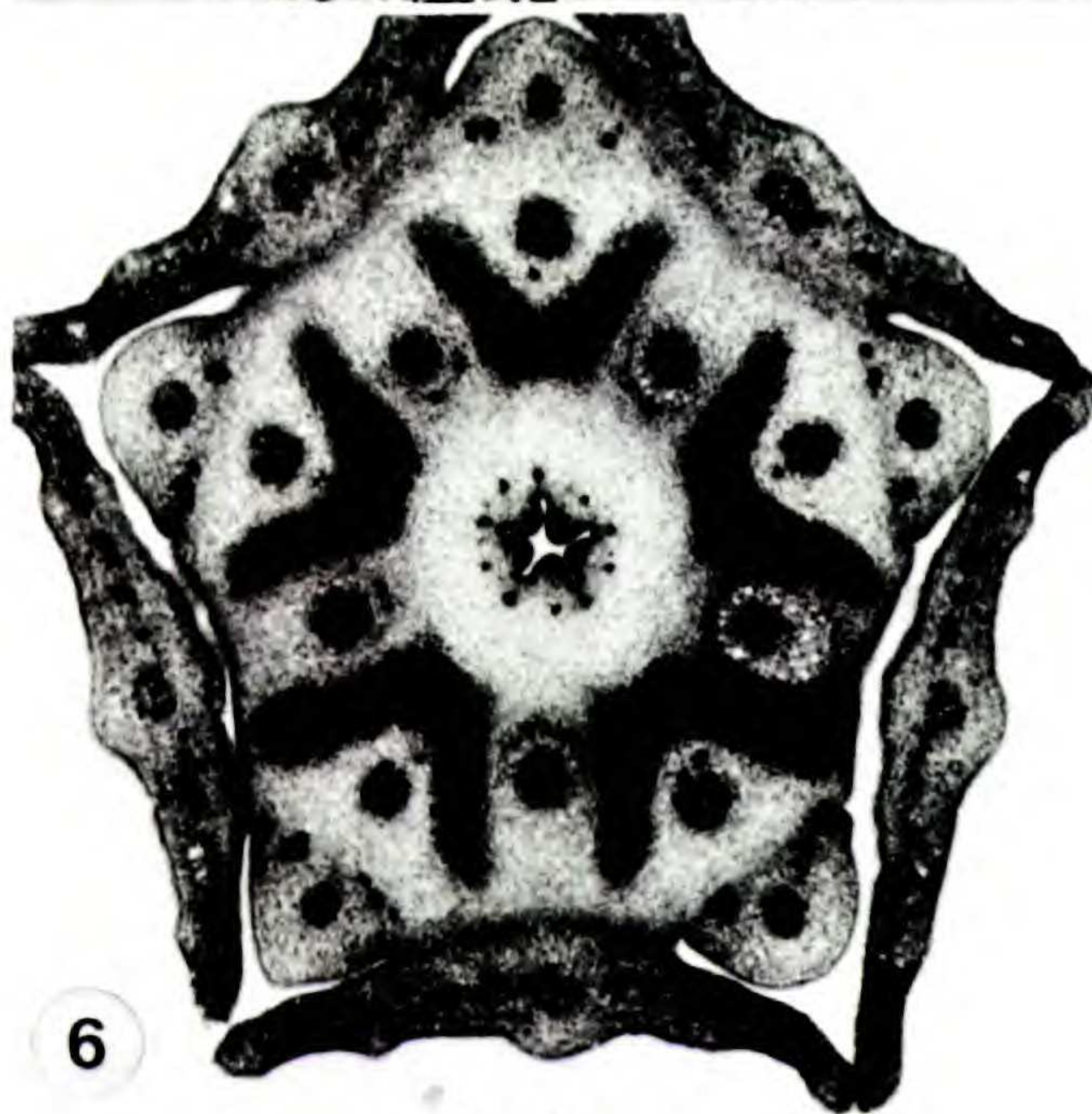
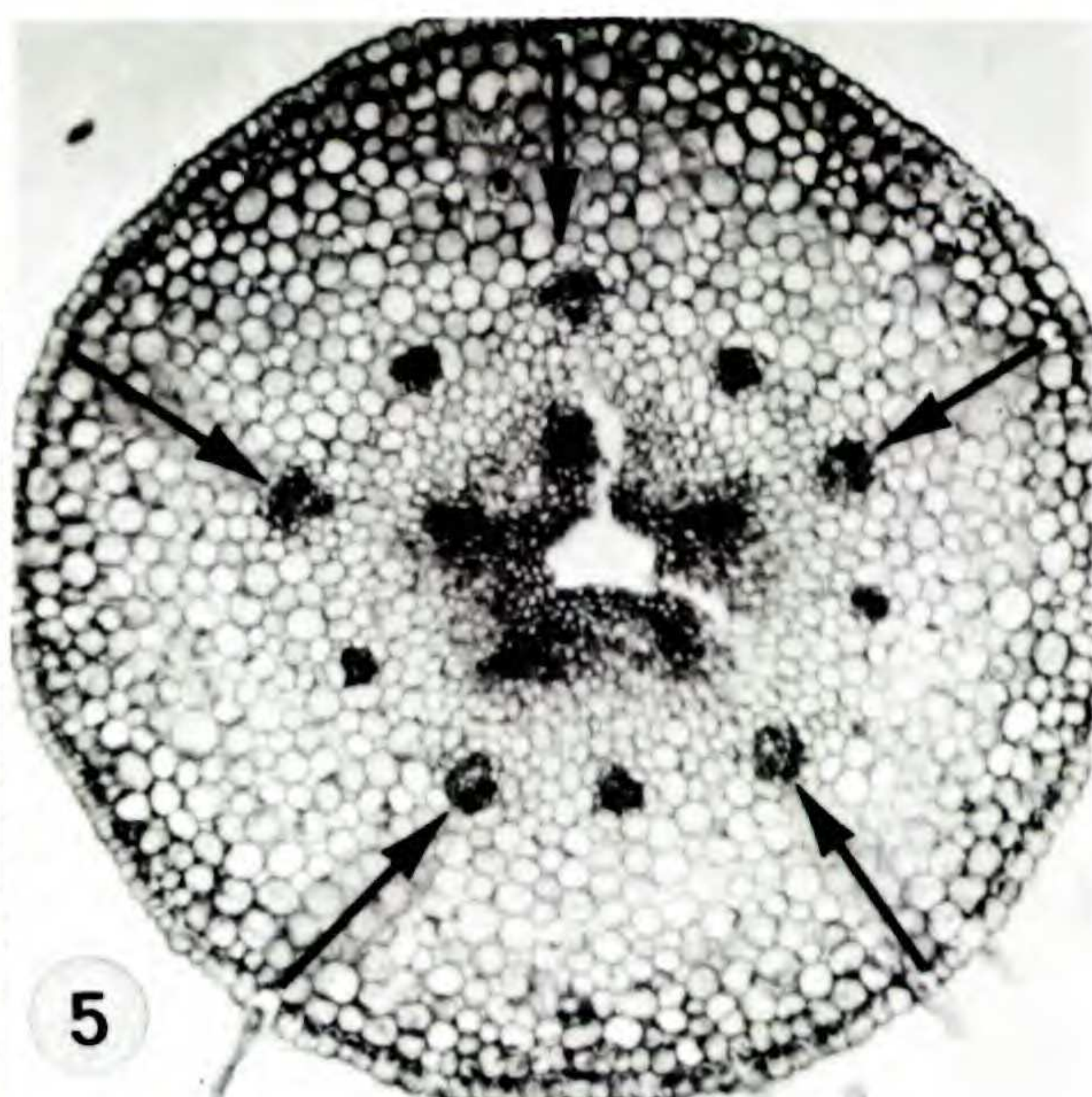
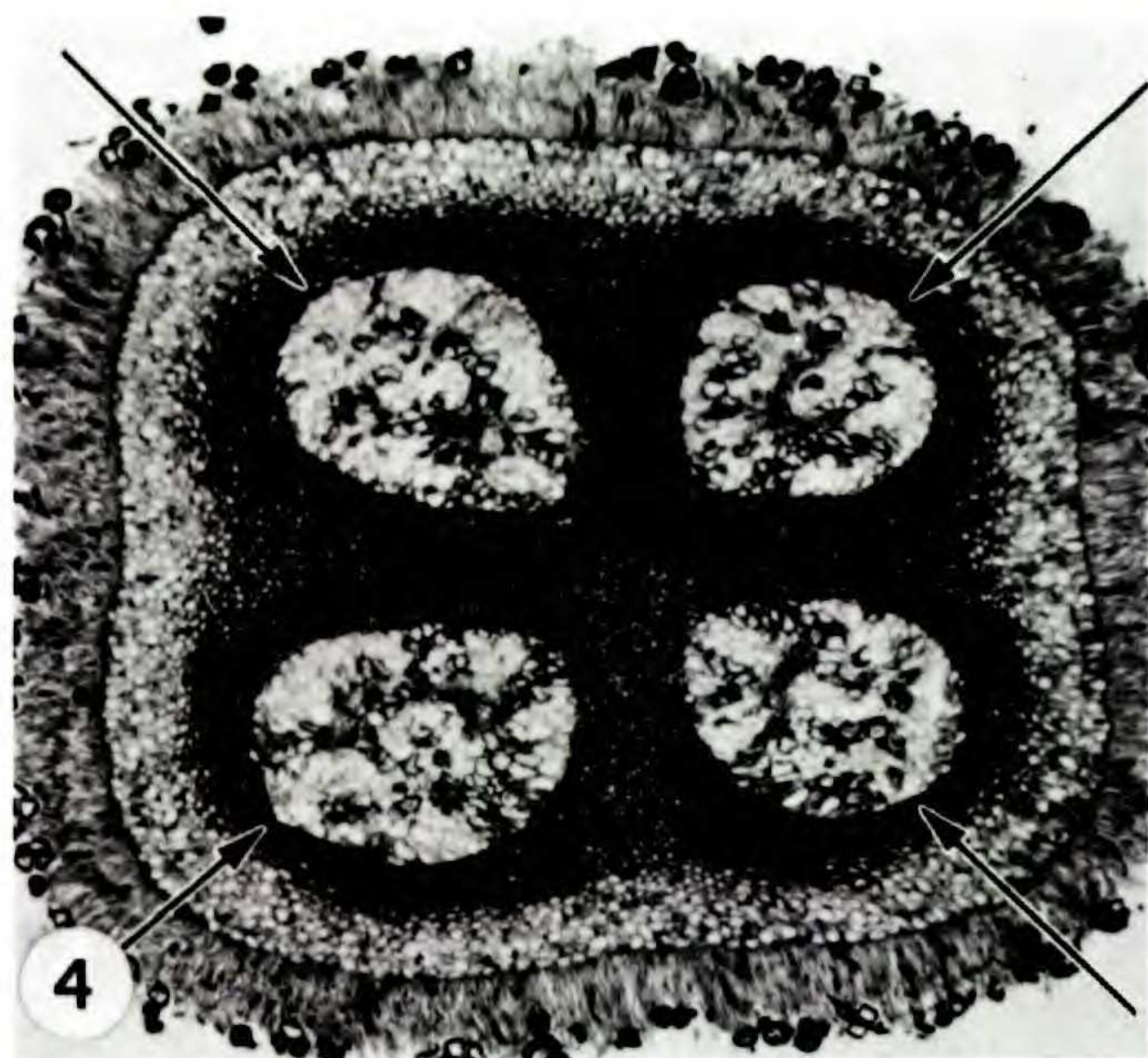
are found in all segregates of the old sect. *Myrtocarpus* (see next paragraph) except *L. densiflora*, in all other diplostemonous ludwigias that I examined, and in some of the haplostemonous ludwigias. The summit of the ovary is less elevated in some of these taxa than in others. Where the summit is not markedly elevated, a cross-section can pass through the whole nectariferous V. Feldhofen (1933) included *Ludwigia peruviana* (as *Jussieua Sprengeri*) in his survey of the structure and secretory function of dicotyledonous nectaries. His fig. 133 is a photographic counterpart of Fig. 3b, and his fig. 134 is a cross-section of one nectary enlarged to show histological details, among them an extensive network of fine bundles connecting basally with all eight stamen bundles.

SIMILAR SPECIES

Emphasizing biosystematic differences, Ramamoorthy (1979) splits the assemblage of species that Raven (1963) assigned to sect. *Myrtocarpus* into seven sections. Except for sect. *Amazonia* (*Ludwigia densiflora*), to be treated later, the flowers of all these sections are outwardly alike, and the outward resemblance is matched by similarity in floral vasculature. I found floral vascular systems throughout the assemblage to be much like that of *L. peruviana* in sect. *Myrtocarpus* sensu stricto.

The vascular differences that do occur do not correlate with the biosystematic differences. To be sure, *Ludwigia foliobracteolata* is like its close relative *L. peruviana* in that the bundles of the petal radii are separate for much of their length (see Fig. 2) and that the style base contains major and minor bundles. But *L. foliobracteolata*'s minor style bundles join the nearest stamen bundles well below the girdle, which is weakly developed when compared with that of *L. peruviana* or with that of almost any other ludwigia. In Ramamoorthy's sect. *Pterocaulon*, *L. decurrens* has the strongly developed central system seen in ovaries of sect. *Myrtocarpus* s. str., but the central system of *L. erecta*, also in sect. *Pterocaulon*, is nothing but a few slender strands at anthesis. The 8-bundle supply to the 4-merous style base is another detail in which *L. decurrens* resembles *L. peruviana* and *L. foliobracteolata*. Style bundles of the septal radii join the stamen supply below the girdle, as in *L. foliobracteolata*. I found no minor style bundles in my liquid-preserved material of *L. erecta* or in herbarium material of the *Myrtocarpus* species *L. tomentosa*—cleared flowers from Ratter & Ramos 215 (NY), sectioned flowers from Dawson 15154 (RSA), and Gardner 2571 (US), all collected in Brazil. Transseptal bundles of *L. decurrens* and *L. erecta* tend to run straight through the cross-sections, unlike those of *L. peruviana*, perhaps because the *Pterocaulon* species have smaller and more linear ovaries.

The bundles of *Ludwigia latifolia*, now sect. *Tectiflora*'s only species, are much like those of *L. peruviana* except in the locular radii, where they unite at a higher level than they do in *L. peruviana*. In most quadrants a major style bundle joins a petal bundle and an antepetalous stamen bundle in or near the girdle, their downward continuation being one big bundle. Occasionally, the style bundle keeps its individuality for some distance below the girdle, as in the upper left quadrant of fig. 3 of my previous article (Eyde, 1978). In *L. latifolia*, as in *L. peruviana*, there are minor style bundles at the level of Fig. 2b; they seem to join the antesealous stamen bundles a little below the girdle.



LUDWIGIA DENSIFLORA

Despite its former inclusion in sect. *Myrtocarpus* (Munz, 1942, 1947; Raven, 1963), *Ludwigia densiflora* had long been considered an isolated or aberrant member of that section, and the list of its peculiarities was lengthened recently (Eyde, 1978); consequently, its reclassification as the only species of sect. *Amazonia* Ramamoorthy (1979) is welcome. The distinctness of the species is further indicated by its floral vascular system. Here the petal midveins do not continue downward into the ovary wall, as they do in *L. peruviana* (Fig. 2). Instead, each ends proximally in the girdle. It will be seen that this occurs in some other ludwigias but they are remote from sect. *Myrtocarpus*, old sense or new. *Ludwigia densiflora* is also aberrant in that the outer bundles in the septal radii—that is, the basal extensions of the sepal midveins—develop massive aggregations of fibers. The fibers are laid down in files, apparently through cambial activity starting at the bundle's periphery before anthesis and continuing thereafter. As the fruit matures, the fibers acquire thicker walls and become lignified. In cross-section each aggregation is then a woody arc 15–20 cells deep and more than 50 cells across. The “woody capsule” of *L. densiflora* is consequently oddly constructed, its woody character deriving from the four to six (depending on merism) major vascular bundles. This is another species in which I found no minor style bundles.

There are depressions in front of the antepetalous stamens in *Ludwigia densiflora* as in *L. peruviana*. Here, however, the ovary's summit is flat, not raised—“disc plane” in Munz's treatments—and the depressions are elliptic or crescentic in cross-sections. They are much smaller than the V-shaped nectaries of *L. peruviana* even when allowance is made for the difference in floral size, and in my material they are hairless (Munz, 1974, says subglabrous). I would be led to infer that this highly self-pollinating species (Ramamoorthy, 1979) secretes no nectar were it not for two other observations: the depressions are lined with densely staining cells and they overlie a phloem network.

SECTIONS *MACROCARPON* AND *AFRICANA*

As regards floral vasculature, these taxa are much alike even though, all things considered, they are not close allies. They are also much like *Ludwigia peruviana* except that central bundles are not obvious in sectioned flowers of sects. *Macrocarpon* and *Africana*. I judge from examining cleared flowers, however, that central longitudinal strands are not altogether wanting, at least in the lower part

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FIGURES 4–9. *Ludwigia* flowers in cross-section.—4. *L. peruviana*, Steinberg s.n. Stigma. Section like the one shown diagrammatically in 3a. Same histological zonation is found in all *Ludwigia* stigmas. Four ovate regions contain the feathery vascular supply. Arrows mark locular radii. $\times 23$.—5. *L. peploides*, Raven 14529. Style with major (arrows) and minor bundles. $\times 100$.—6. *L. peploides*, Raven 26493. Ovary's summit not elevated. Section passes through densely stained V-shaped regions underlying the nectaries. $\times 36$.—7. Same flower, 150 μm lower. Shows almost all of vascular girdle in one transverse plane. $\times 35$.—8. Same collection, different flower. Slightly oblique section shows lateral bundles of sepal joining petal midveins (arrows) in girdle. $\times 35$.—9. *L. peploides*, Raven 14529. Transverse bundle connects nectary's vascular network with antepetalous stamen bundle. Antesepalous stamen bundles (arrows) also contribute to nectary supply. $\times 46$.

of the flower. In cross-section a fine, long, central strand is not easily distinguished from short strands connecting the transseptal bundles with the placentas, and dislocated raphides in the central part of the flower may make it impossible to follow any of these bundles for more than three or four microtome sections.

My material of *Ludwigia neograndiflora* and *L. octovalvis*—sect. *Macrocarpon*—has style bundles in the locular radii only. In *L. octovalvis* these bundles link basally with the antepetalous stamen bundles about 1 mm below the girdle in an inferior ovary (“hypanthium”) 10 mm or so in length; in *L. neograndiflora* this junction is about a third of the way down the ovary. Similarly, the union of the antepetalous stamen supply with the petal supply is about one-third of the way down the ovary in *L. octovalvis*, about two-thirds of the way in *L. neograndiflora*. As in most ludwigias, bundles supplying antesepalous stamens join the extended sepal midveins near the base of the flower.

I know the two species of sect. *Africana* only as herbarium specimens. My cleared flowers of *Ludwigia stenorrhapha* (Brenan) Hara came from *Wood 5341* (US), Natal, sectioned flowers from *Dümmer 2738* (US), Uganda; cleared flowers and sectioned flowers of *L. jussiaeoides* Desr. from *Holst 2972* (US), Tanzania. I found no style bundles in the septal radii of *L. stenorrhapha*. The style bundles in the locular radii converge on the antepetalous stamen bundles and the petal bundles a short distance below the girdle. The three bundles come together about a tenth of the way down the inferior ovary. *Ludwigia jussiaeoides* has style bundles in the septal radii, but they are tenuous, each having only two or three tracheary elements in cross-section. I do not know where these slender strands hook up basally because they are hard to follow through the fine network supplying the nectaries; possibly they join basally with that network. As in *L. stenorrhapha*, the style bundles of the locular radii join the petal bundles a little below the girdle (less than a tenth of the way down the ovary). Here, however, there are only two bundles involved, for *L. jussiaeoides* is haplostemonous. The antepetalous stamens and their bundles are missing.

LUDWIGIA PERENNIS

Raven (1963) erected sect. *Caryophylloidea* for the haplostemonous species *Ludwigia perennis* L., citing “ribs on the fruit not being prominent” as one of its distinctions. It is a vascular distinction. Fruits of *L. perennis* have fewer ribs than those of *L. jussiaeoides*, for example, because the ovaries of *L. perennis* are only scantily vascularized in the locular radii. My sections of herbarium flowers—*Morse 275*, Guangxi (US)—show slender strands only two or three tracheary elements thick in some locular radii, no strands in other locular radii. The base of the style has a bundle in each locular radius (none in the septal radii), but I can not tell from my micropreparations how this bundle connects with other parts of the vascular system. The girdle is weakly developed. The central system, much of it concentrated in one large strand, is apparently the important supply to the placentas; transseptal bundles are equally hard to find in microtomed flowers and in cleared flowers. Raynal’s (1966) description of *L. perennis* says the summit of the ovary has four glabrous, nectariferous dimples (fossettes) in front of the petals, but her illustration (pl. 18, fig. 4) does not show the dimples nor does it show that the summit is elevated. In my preparations, which include good

longitudinal sections, the summit of the ovary is both glabrous and raised, and the antepetalous quadrants bulge out between the stamens. The dimples, each a shallow depression on the surface of an interstaminal bulge, are evident in some of my preparations but not others.

ENDOCARP TAXA

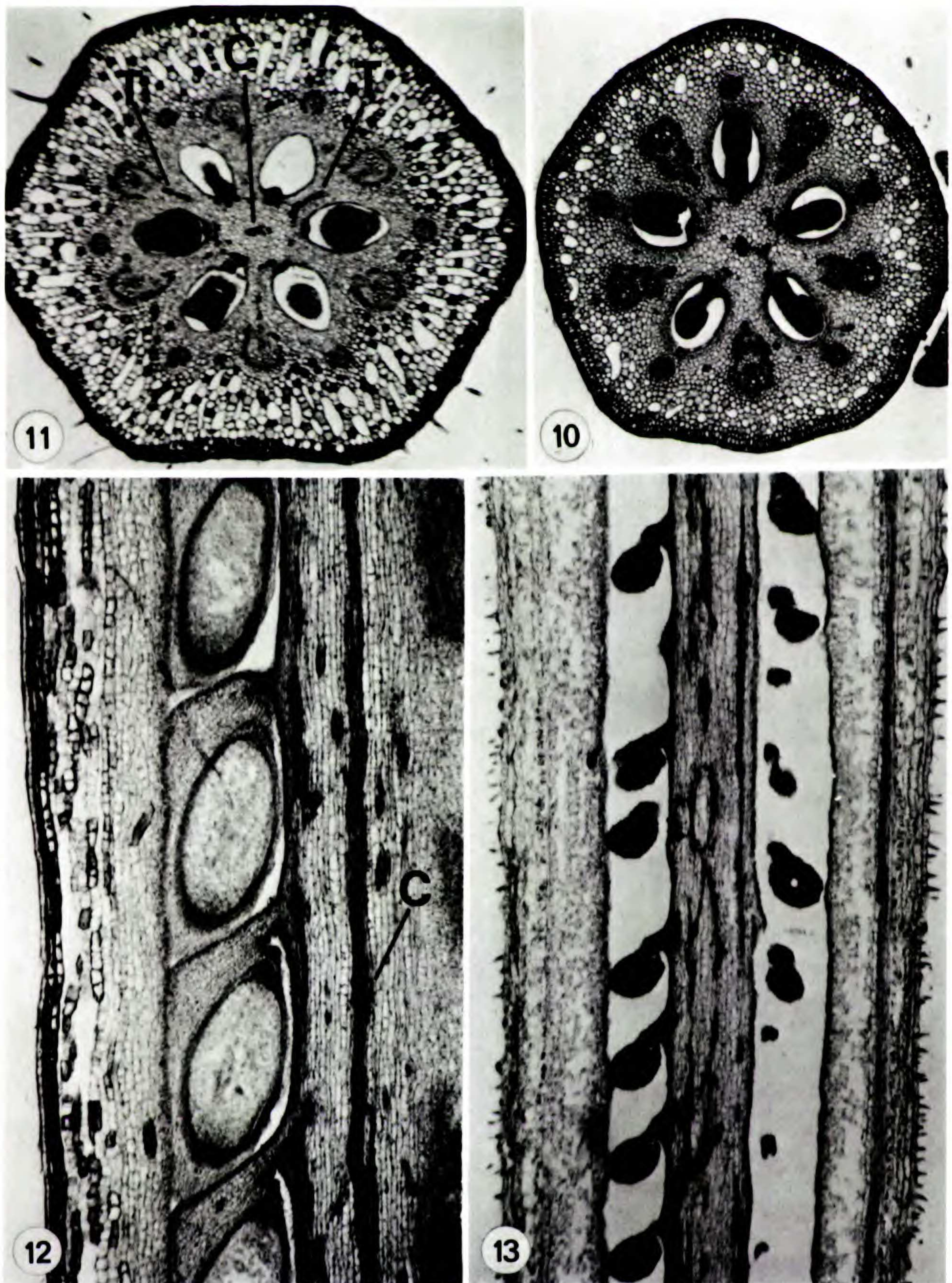
Ludwigias with endocarp-clad seeds fall into two main groups (Raven, 1963; Eyde, 1978). In one of these groups, a natural assemblage comprising sect. *Oligospermum* and *Ludwigia torulosa*, cells linking the locules fuse with outer cells of the testa as the fruit develops. The other endocarp group, with seeds free at maturity, may embrace more than one evolutionary lineage; it comprises sect. *Seminuda* plus *L. abyssinica*, *L. epilobioides*, and *L. hyssopifolia*.

Floral vasculature of sect. *Oligospermum* differs from that of the ludwigias so far treated in that the two big bundles in each septal radius unite more or less at the median level of the inferior ovary, not at its base. In my material these two bundles commonly merge more or less at the median level of the ovary. In a sectioned flower of *Ludwigia peploides* with columns of 22 ovules or so in each locule the big septal bundles merge opposite the ninth ovule down. In a flower of *L. uruguayensis* with 12–14 1-seriate ovules per locule, they merge opposite the sixth ovule down. Microtome sections taken below this junction show one large bundle in each septal radius, a bundle outlined first by phloem patches, later by a more or less continuous layer of tanniferous cells. But within each sectioned bundle there is an inner and an outer patch of thick-walled longitudinal fibers; the appearance in a cleared preparation is consequently that of two closely juxtaposed bundles extending to the base of the flower. As the fruit develops, the number of fibers increases, partly by division of bundle parenchyma cells, and the appearance of duality is gradually lost (see the massive bundles in Eyde, 1978: fig. 17).

Petal midveins of sect. *Oligospermum* end basally in the girdle like those of *Ludwigia densiflora*. My preparations of *L. peploides* and *L. uruguayensis* show some of the petal laterals merging basally with the girdle near its junction with the petal midvein. I have not observed this in other ludwigias. Ordinarily, petal laterals merge with the petal midvein at the girdle or a little above it as in *L. peruviana*.

The major style bundles of *Ludwigia peploides* join the antepetalous stamen bundles at the level of the sixth or seventh ovule down. In *L. uruguayensis* the junction is at the level of the third or fourth ovule. Again, these observations are from sections. In cleared material the junctions seem to be lower in the flower. *Ludwigia peploides* has minor style bundles in the septal radii (Fig. 5). Conspicuous in all my preparations from this species, they usually join the antesealous stamen bundles below the girdle, at the level of the first ovule or a little above it; however, Fig. 8 shows one merging with a stamen bundle a little above the girdle. Oddly, I have not found septal bundles in the styles of *L. uruguayensis* to match those of *L. peploides*.

Ovules of *Oligospermum* species are supplied via the central route (Figs. 10, 12) and by a much-branched network of fine transseptal bundles. A difference with *Ludwigia peruviana* is that all the main transseptal bundles, even the up-



FIGURES 10-13. Sectioned *Ludwigia* flowers.—10. *L. peploides*, Raven 14529. Cross-section with central bundle supplying ovules. $\times 46$.—11. *L. uruguayensis*, Raven s.n. Cross-section showing central bundle (C) and two transseptal bundles (T). $\times 33$.—12. *L. peploides*, Raven 14529. Longitudinal section of ovary, central bundle prominent. $\times 50$.—13. *L. leptocarpa*, Raven 26491. Longitudinal section of ovary, central supply a network. $\times 46$.

permost ones, rise through the septa at an angle—mostly 30–45 degrees from vertical. As the same is true of most other endocarp taxa, the difference probably relates to the ontogenetic elongation of the inferior ovary in these plants.

Oligospermum ovaries are flat-topped. Accordingly, the V-shaped nectariferous grooves are more or less horizontal with respect to the flower's axis (Figs. 6, 9). Elsewhere in the genus elevation of the summit can vary from one member of a section to another. The character is consistent enough, however, to have a place in Munz's keys, where it aids in parting some closely related species (e.g., *Ludwigia affinis* and *L. leptocarpa*).

In floral cross-sections of *Ludwigia torulosa* the sepal midveins and antesealous stamen bundles retain their individuality to the base of the flower. The septal pairs do not merge proximally in one large bundle, as they do in sect. *Oligospermum*, at least not in the limited herbarium material that I have examined, and the septal bundles of a mature *L. torulosa* fruit are not massive like those of an *Oligospermum* fruit (compare Fig. 19 with fig. 17 in Eyde, 1978). Petal midveins of *L. torulosa* vary in the way they terminate. Some end proximally in the girdle; others continue down through the ovary wall to the base of the flower. Style bundles occur only in the locular radii. They join the petal bundles in the upper part of the ovary wall or, where a downward continuation of the petal midvein is wanting, continue alone to the flower's base. As in sect. *Oligospermum*, ovules are supplied by the central route and by the transseptal route. The summit of the ovary is divided into five or six swollen lobes by the single whorl of stamens. Traversing each lobe is a deep, gently curved nectary tightly roofed over by a protruding crest of trichomes.

My two collections of *Ludwigia leptocarpa* differ somewhat with respect to vasculature. The big septal bundles retain a distinct duality down to the flower's base in all specimens, whether sectioned or cleared, but there are individual differences in the locular radii. In *Chevalier 21* the major style bundles join the stamen bundles at the girdle or above it. In *Raven 26491* the bundles merge below the girdle—as low as the twelfth ovule down in a column of 75–80 ovules. The petal midveins of both collections end in the girdle and both collections have a well-developed, steeply rising transseptal system. Both collections have bundles in the septal radii of the style base. Those of *Raven 26491* are a series of slender, irregularly oriented strands. Because of their irregularity and spacing, they might well be considered a distal continuation of the transseptal system. In contrast the minor style bundles of *Chevalier 21* are solitary strands like those of *L. peruviana*, but stelar vasculature is not perfectly symmetrical in this collection. The major and minor bundles together are one or two fewer than the combined septal and locular radii, and a bundle can shift from one radius to an adjoining radius when followed through a series of cross-sections. The minor style bundles of both collections merge with stamen bundles at the girdle level or very near it. A nice vascular distinction separates my material of *L. leptocarpa* from that of sect. *Oligospermum*. *Oligospermum*'s central system is largely concentrated in one big strand running most of the length of the ovary, whereas the central system of *L. leptocarpa* is a loose network (compare Figs. 12, 13).

In order to include a second *Seminuda* species, I looked at cleared flowers and sectioned flowers from herbarium specimens of *Ludwigia affinis* (DC.) Hara:

Philipson, Idrobo & Fernández 1620, Colombia (US). As one would expect, floral vasculature is like that of *L. leptocarpa*. The big septal bundles are separate all the way down. Petal midveins end in the girdle. Ovules are supplied by steeply rising transseptal strands in addition to a conspicuous central system that is somewhat more centralized than the reticulate central system of *L. leptocarpa*. Major style bundles, all symmetrically placed, link with the stamen bundles below the girdle, at the level of the uppermost ovule or two. I can not identify minor style bundles in sections of *L. affinis*, and they are just visible enough in my cleared flowers that I can say they are there and nothing more.

Nectaries of *Ludwigia affinis*, like those of *L. leptocarpa*, are hairy inverted V's. Raven (1963) described those of *L. africana* (Brenan) Hara, also in sect. *Seminuda*, as glabrous. A hairless nectary seems out of place in a close relative of *L. leptocarpa* and *L. affinis*, so I looked at rehydrated flowers of *L. africana*—*Zenker & Staudt 323*, Cameroon (US)—and I found long hairs fringing the nectaries.

Floral vasculature of *Ludwigia abyssinica* A. Rich., sect. *Cryptosperma*'s only species, does not differ greatly from that of *L. affinis* or *L. leptocarpa*. Herbarium flowers from *Baldwin 9734*, Guinea (US), show two bundles in each septal radius all the way to the bottom of the flower. They have neither stamens nor stamen bundles in the locular radii and there are no minor style bundles. Major style bundles merge with the petal midveins in the girdle and stop there; I find no bundles in the locular radii below the girdle, where the wall of the inferior ovary is only about six cells thick. The central system and the steeply rising transseptal system are both well developed. According to Raven (1963) and Raynal (1966), nectaries of *L. abyssinica* are usually fringed with short hairs, but the nectaries of this collection seem to be altogether glabrous.

Septal radii of *Ludwigia hyssopifolia* have the usual two bundles. Despite the narrowness of the ovary, these bundles retain their individuality more or less to the base of the ovary. Central bundles supplying the ovules can be seen dimly in my cleared herbarium flowers, and transseptal bundles can be seen with some difficulty in the microtomed flowers. There are no minor style bundles. The major style bundles join the antepetalous stamen bundles and the extended petal midveins a little below the girdle, where they merge in a single strand that can be followed downward in the locular plane to the flower's base. As the fruit matures, these solitary bundles are more or less enclosed by the hard endocarp tissue that forms around the lower part of each locule, where seeds are 1-seriate. Each bundle then becomes a line of weakness along which the dispersed endocarp units eventually split. This halving of the endocarp unit is unique to *L. hyssopifolia*.

Early in the investigation Raven pointed out to me that fruits of *Ludwigia abyssinica*, *L. epilobioides*, and *L. hyssopifolia* are not heavily ribbed or fluted like *Seminuda* fruits (see Raven, 1963, figs. 4–6; Ormond et al., 1978, figs. 2–3). The ribbed appearance is an external expression of the eight (or 10 or 12) big bundles directly underlying the surface, those of the locular radii contributing to the effect because they are pressed outward when the hard endocarp units form. This is also the reason for the heart-shaped outline of a *Seminuda* endocarp unit (Eyde, 1978: figs. 35–36): the lobes of the heart take form with the big bundle of the locular radius between them. In *L. hyssopifolia* the bundles of the locular

radii are not seen externally as ribs because in the lower part of the fruit they are at least partially imbedded in the endocarp tissue and in the upper part there is no hard endocarp. Fruits of *L. abyssinica* are not heavily ribbed because they grow from flowers that have no bundles in the locular radii, and the same is true of *L. epilobioides*.

There are no bundles in the locular radii of my herbarium flowers of *Ludwigia epilobioides*—microtome sections from *Lei 993*, Hainan Xingzhengqu, and *Chien 207*, Jiangsu; cleared flowers from the *Lei* collection and from *Shimadzu Co. s.n.*, Japan (all US). Fruits of this species sometimes have short, irregular bundles in the locular radii, but these are late-developing branches from the outer septal bundles. The ovary wall, like that of *L. abyssinica*, is only about six cells thick in the locular radius (in *L. hyssopifolia*, the thickness is 10–12 cells). Duality of the septal vascular supply is difficult to detect in my cleared preparations; that is, each septal radius seems to contain one heavy strand. Most of my microtomed flowers agree with the cleared flowers, showing the antesealous stamen bundle and the sepal midvein merging in a heavy strand at the girdle level, but one flower from *Chien 207* has these bundles separate almost to the peduncle. Style bundles, poorly developed and hard to follow, seem to link with the girdle. As this is one of the haplostemonous ludwigias, there are no antepetalous stamen bundles. Petals of *L. epilobioides* are small, and I was not able to find and follow the midveins in microtome sections or in cleared material. With a hand lens, however, I can see petal midveins on some herbarium sheets, and I must assume they end basally in the girdle, because the locular radii are bundle-free below the girdle. The central supply to the ovules is unusually heavy, and it fills much of the ovary's axis; consequently, little or no endocarp tissue develops on the inner side of the locules (Raven, 1963: fig. 6). I judge from the appearance of cross-sections that the endocarp forms completely around the locules in the upper part of the ovary and that the thin inner side then splits as the fruit matures. In the lower part of the ovary, the endocarp seems never to form on the inner side of a locule. Though the transseptal supply is relatively weak in *L. epilobioides*, my cleared flowers show some strands. They are in the lower part of the ovary, and they rise at the sharp angle seen in other species with long, slender ovaries.

The overall similarities of the Southeast Asian species *Ludwigia prostrata* Roxb., alone in sect. *Nematopyxis*, are with the endocarp taxa, even though its fruits do not have a hard endocarp layer. With 1-seriate seeds and no hard endocarp, *L. prostrata* seems to contradict my claim that endocarp formation and single-file seeds are linked developmentally (Eyde, 1978). The wall of the thread-like inferior ovary of this species is so thin, however, that endocarp formation may be out of the question. Moreover, the ovules are not neatly 1-seriate like those of *Seminuda* and *Oligospermum*. My serially sectioned flowers from *Belcher LI-C-498*, Assam (US), show crowding of the ovules in the upper part of the ovary. The condition is reminiscent of *L. epilobioides*, though the two species differ substantially in other respects. Not surprisingly, in view of the thin wall, the inferior ovary of *L. prostrata* has no vascular bundles in the locular radii. The petal midveins end in the girdle, and there are no antepetalous stamen bundles because the flowers are haplostemonous. Furthermore, *L. prostrata* has no style bundles at all in the locular radii. Instead, the style base is vascularized

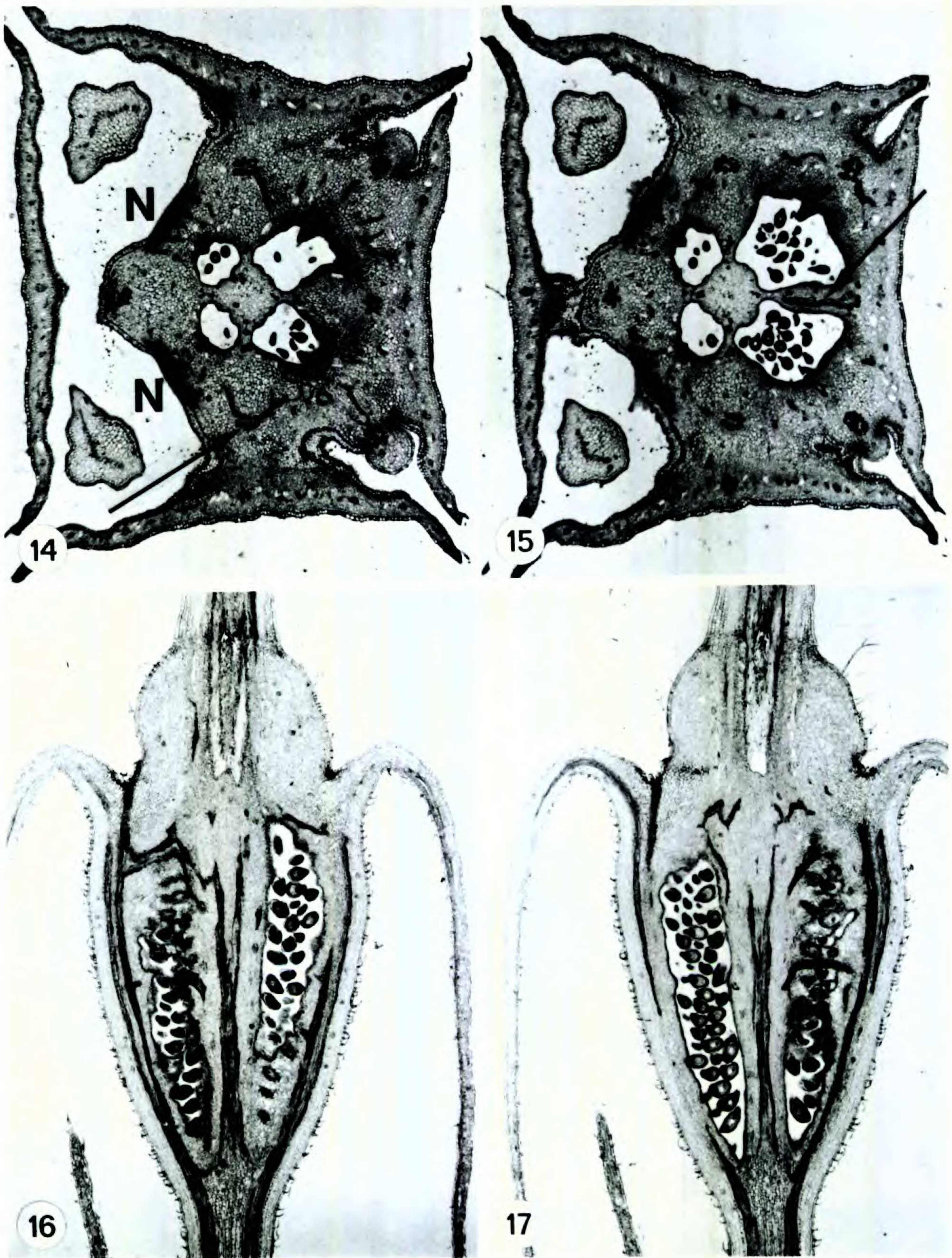
only by bundles corresponding to the minor style bundles of *L. peruviana* or of *L. peploides*. Placentas are supplied by a central system that shows up nicely in my cleared flowers; these, like the sections, are from the Belcher collection. None of my preparations, cleared or cut, show transseptal strands unequivocally. The nectaries are shallow, upright depressions on the ovary's elevated summit. Raven (1963) called them glabrous, but every one I have looked at has a thin skirt of long hairs across the upper edge. One of five microtomed flowers turned out to be 5-merous, a condition not reported before for this ordinarily 4-merous species.

SECTION *LUDWIGIA*

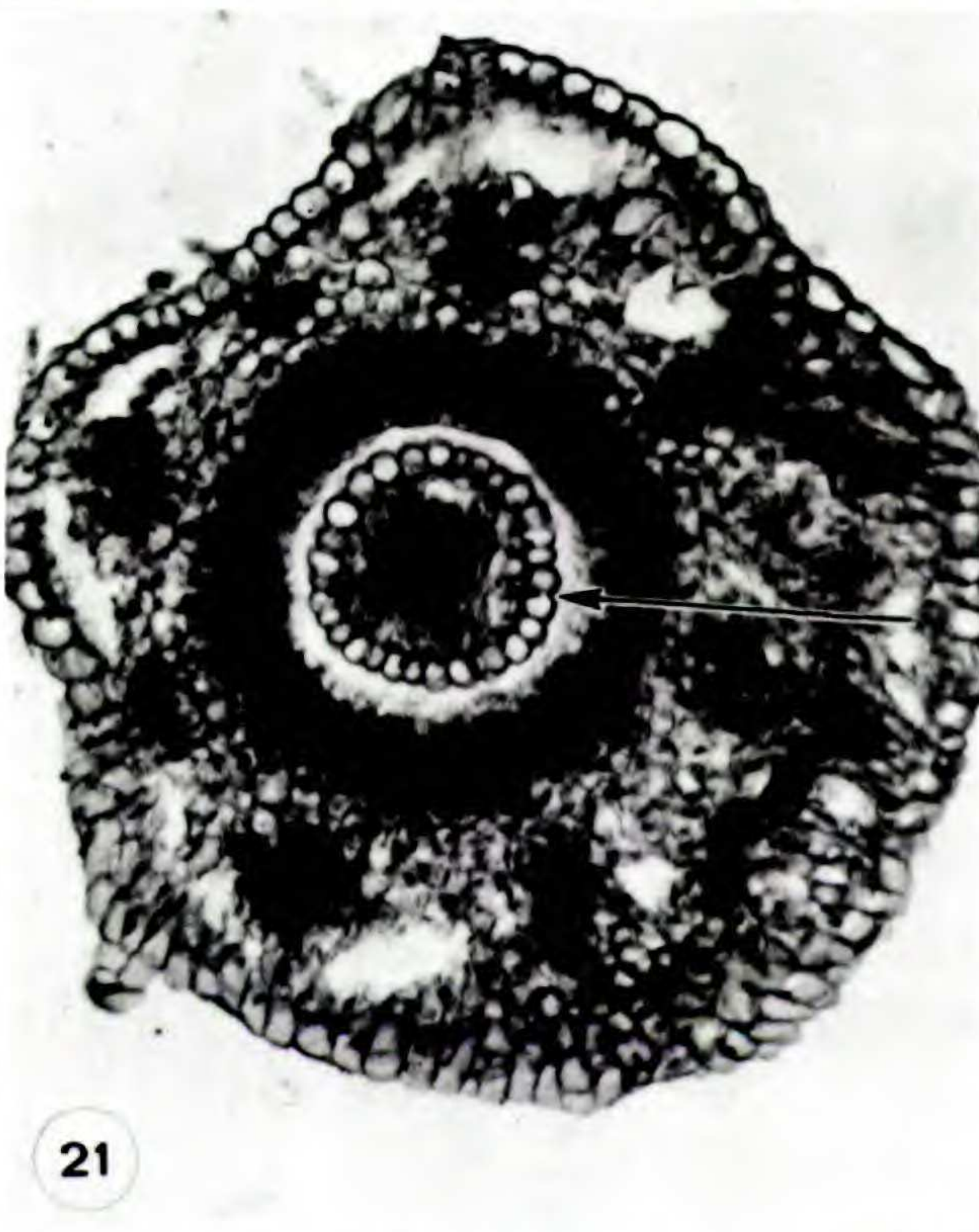
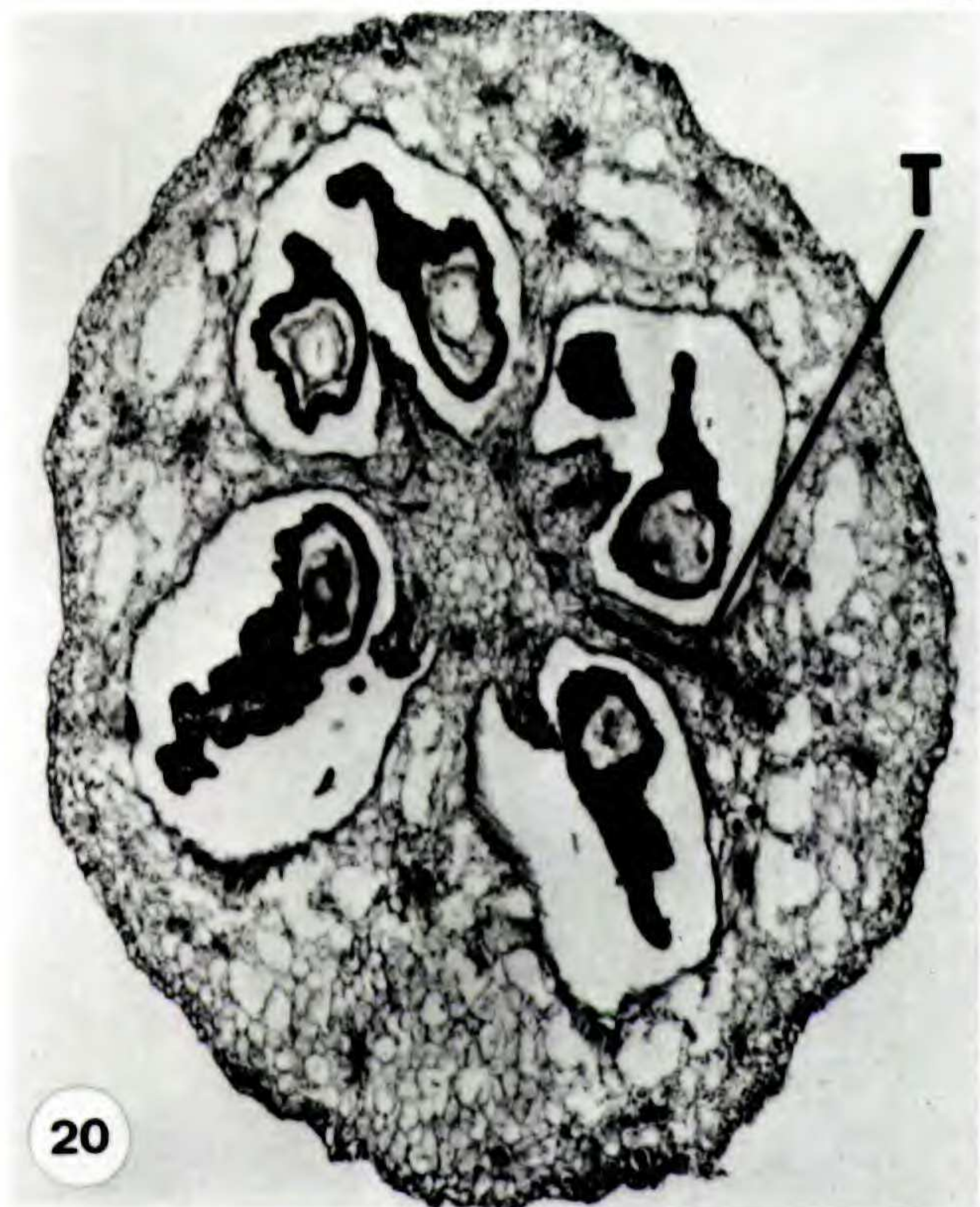
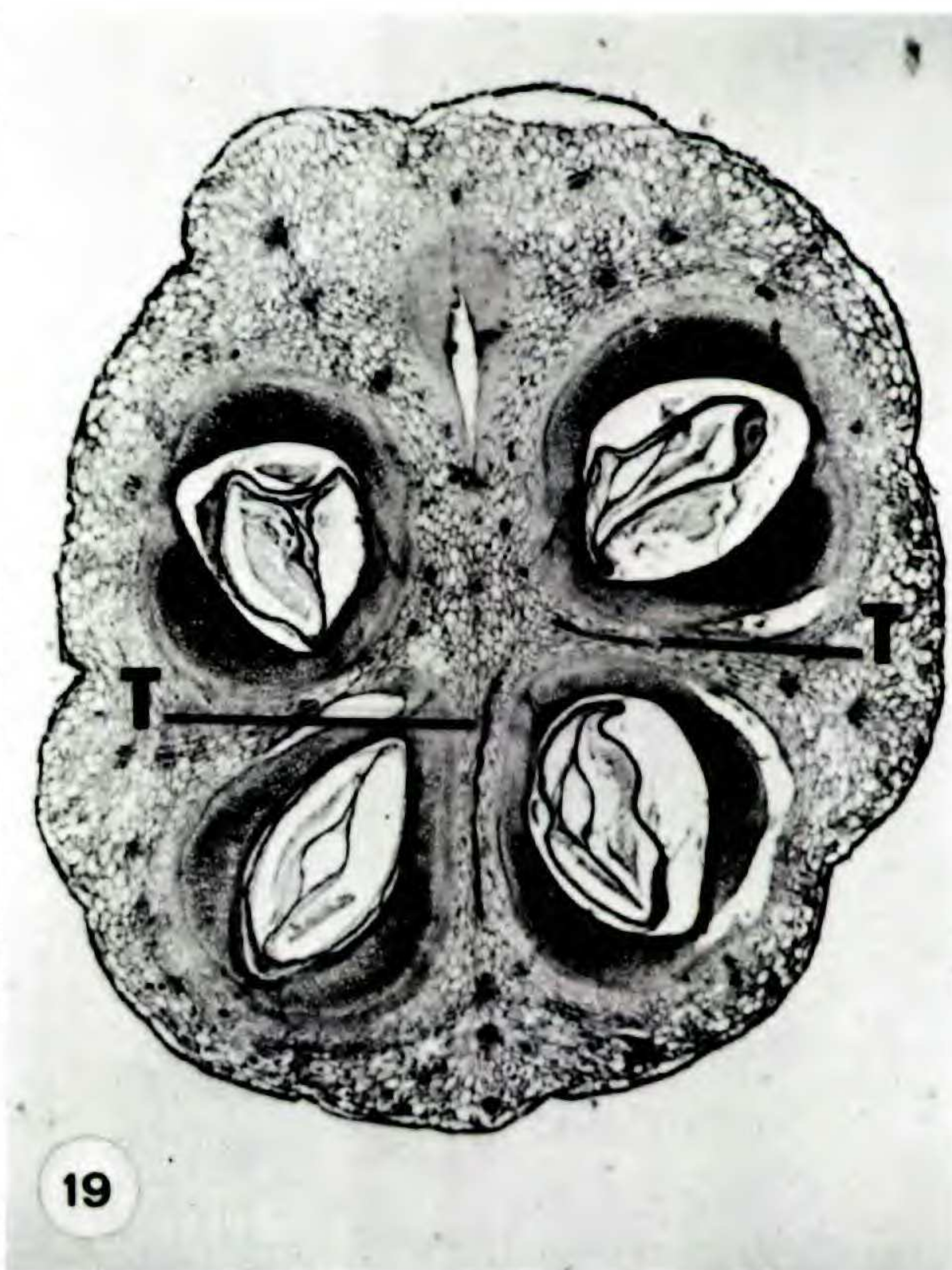
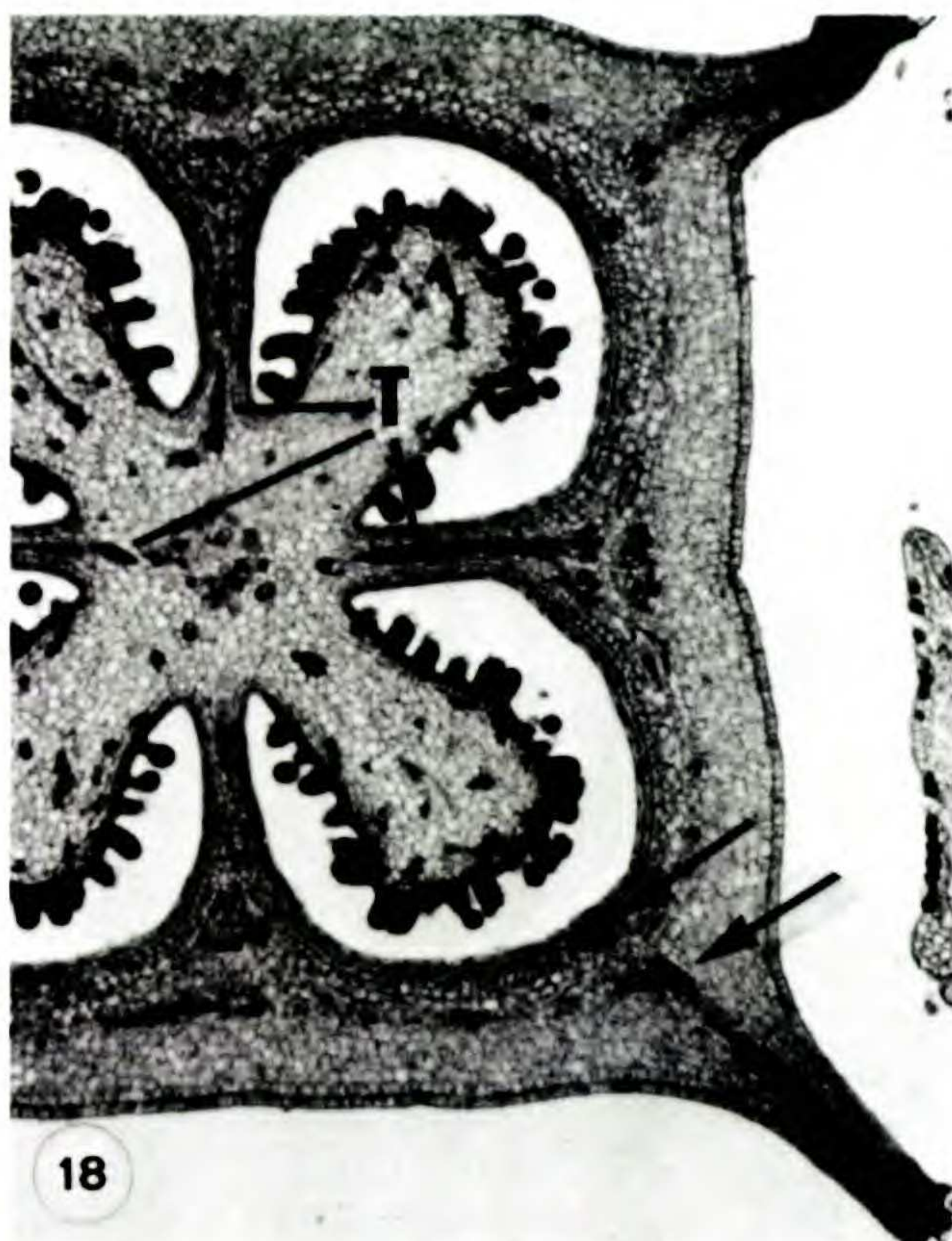
Examining flowers of three of the four species in this haplostemonous section—*Ludwigia alternifolia*, *L. maritima*, *L. virgata*—I found almost identical vascular systems. Sepal supply and stamen supply are separate to the flower's base (Fig. 16), as is true of ludwigias in general. In addition the four big style bundles and the four petal bundles can be followed downward as independent bundles for half the length of the ovary or more (Fig. 18). This uncommon condition seems to be related to the angular or winged outline of the inferior ovary. The angles develop below the margins of the broadening sepals, and two bundles differentiating in the same radius are kept apart by the lateral growth that produces the angles. In *L. alternifolia*, where the angles are especially prominent, each is vascularized by a series of short transverse strands connecting like the rungs of a ladder with the petal supply. In the septal radii of *L. alternifolia* short bundles run from the base of the style to each stamen bundle, joining it well above the girdle (Fig. 15), but they are not as well defined or as constant in their occurrence as the minor style bundles of some of the diplostemonous species. The flowers of sect. *Ludwigia* have a strong central system and a transseptal system consisting of a few well-developed transverse bundles (Figs. 16–18). Both systems form early: provascular strands are apparent in a sectioned bud of *L. alternifolia* that was fixed before the ovules had developed. All species of the section have four shallow, but nonetheless prominent, hairless nectaries on the ovary's raised summit. These are abundantly vascularized by a network connected to the four stamen bundles (Fig. 14) and the four major style bundles.

SECTIONS *DANTIA*, *MICROCARPIUM*, *MIQUELIA*

Members of these three sections, all herbaceous and haplostemonous, have smaller flowers than most other ludwigias. Some have no petals, but apetalous does not change the position of the stamens; they remain in front of the sepals as if the petals were present. With or without petals, the nectaries are hairless and are rounded rather than depressed. Where they are best developed, they become four prominent hemispheres around a sunken style base (see Mayr, 1969: 235 for floral ontogeny of *Ludwigia arcuata*, a *Dantia* species with protuberant nectaries). Floral vascular systems are similar in the three sections. All species have the downward extensions of sepal midveins and stamen bundles running separately through the ovary to the base of the flower. Styles contain only the four major bundles, and *L. ovalis* (sect. *Miquelia*) may even lack these, for in this species



FIGURES 14-17. Sectioned *Ludwigia* flowers.—14-15. *L. alternifolia*, Broome 862. Oblique sections with sepal diverging.—14. Shows \pm transverse bundles linking stamen bundle (arrow) with nectaries (N).—15. Cut 50 μ m lower, shows a minor style bundle (arrow) joining a stamen bundle. Both $\times 19$.—16-17. *L. maritima*, Arguelles 1, stamens abscised. Longitudinal sections 30 μ m apart showing dual ovular supply; 16, passing through upper part of thin septum on left, shows heavy transseptal bundles linking stamen bundle with placenta and central supply. Note separation of stamen bundle and sepal bundle in ovary wall, also basal linking of central supply with outer bundles; 17, passing through part of septum on right, shows pieces of two large transseptal bundles. Both $\times 15$.



FIGURES 18–21. Flowers of *Ludwigia* and *Gayophytum* in cross-section.—18. *L. alternifolia*, Broome 860. Note transseptal bundles (T), separation of petal bundles and style bundles (arrows), and prominent central supply. $\times 50$.—19. *L. torulosa*, Cowan 38886. Post-fertilization ovary from pressed specimen, one locule abortive. T's mark transseptal strands. Longitudinal bundles of this species are much thinner than those of *L. peploides* and *L. uruguayensis*. $\times 18$.—20. *L. ovalis*, Boufford 19961, with transseptal bundle (T). Ovary wall is aerenchymatous but there is no evolutionary link with aerenchyma of *Oligospermum* ovaries. $\times 37$.—21. *G. racemosum*, Raven 26420. *Gayophytum* species have no real floral tube but style (arrow) emerges from a depression that has nectariferous tissue on its androecial side. $\times 114$.

the bundles of the locular radii can end distally at the style's base without rising into the style. Nectariferous areas commonly receive a few short branches—mostly supplied by the style bundles—even in the species with less prominent nectaries. The ovules of all species seem to be supplied mainly via the central route, though a transseptal bundle or two can be found in most flowers. The figured cross-section of *L. palustris* in my introductory article (Eyde, 1977: fig. 9) shows a transseptal bundle traversing one of the septa; see also the cross-section of *L. ovalis* in Fig. 20.

The one taxonomically variable feature of floral vasculature worth noting is the degree to which the locular midplane is vascularized. But two species of a section can differ more in this regard than species in different sections, and, contrary to expectation, the flowers with the best-developed bundles in the locular radii—that is to say, in the petal radii—are not those with petals. All my preparations of *Ludwigia alata* (wet collection) have conspicuous bundles running from the style to the girdle, whence they descend to the flower's base. This is also true of most quadrants in the misnamed herb *L. suffruticosa* (US herbarium flowers: Jones 79, Florida), though the bundles of the locular radii are much weaker here. Both are apetalous species belonging to sect. *Microcarpium*. In *L. linearis*, a *Microcarpium* species with petals, style bundles merge with petal midveins in the girdle, and the slender strand descending from each merger attenuates and disappears in the ovary wall. *Ludwigia ovalis*, though apetalous, has bundles of the locular radii ending blindly in the ovary wall like those of *L. linearis*. The other apetalous species that I looked at are *L. palustris* (wet collection) in *Dantia* and, in *Microcarpium*, *L. glandulosa*, *L. pilosa* (wet collections), *L. lanceolata* (Harper 1605, Georgia), *L. polycarpa* (Bissell & Clarke 245, Connecticut), and *L. sphaerocarpa* (Kral 44739, Alabama). In these species the locular segments of the ovary wall are commonly devoid of long vascular bundles, though they may be lightly vascularized by a few fine, irregular branches from the big septal bundles. Style bundles ordinarily end proximally in the girdle, but in *L. pilosa* I have seen at least one style bundle clearly connecting with a sepal lateral bundle just above the latter's junction with the girdle. In *L. arcuata*, a *Dantia* species with petals, bundles of the locular radii vary markedly even within one flower. Some quadrants have the petal midvein merging with the style bundle in the girdle; in other quadrants the petal midvein joins the girdle but its downward continuation merges with the style bundle below the girdle. Below the junction of *L. arcuata*'s style bundle and petal midvein, there can be a slender strand continuing to the flower's base or a diminishing strand ending blindly in the ovary wall; or, when petal midvein and style bundle merge in the girdle, a downward extension can be lacking.

VASCULAR DIFFERENCES DISCUSSED

Except in sect. *Oligospermum*, where the partial loss of duality seems to be ontogenetically and phyletically secondary, the big bundles of the septal radii are separate to the flower's base. This is not true throughout the family. Kowalewicz (1956) found and I have confirmed that the septal bundles of *Epilobium hirsutum* (the D bundles of Bonner, 1948) are not as markedly divided as those of *Oenothera* species, where, Kowalewicz pointed out, the ovary wall is thicker. Simi-

larly, the bundles are double in the large flowers of *Hauya*, single in the small flowers of *Circaea*. But the distinction is not wholly a matter of wall thickness and flower size, for the septal bundles are double even in the threadlike ovaries of *Ludwigia prostrata* and in such small-flowered ludwigias as *L. ovalis*. It depends more, I think, on the timing of development of floral parts relative to each other. Onagraceous petals are slow to develop and in some species they are not even initiated until the antesealous stamens have begun their development (Payer, 1857: 485; Mayr, 1969). In *L. uruguayensis* ("Jussiaea grandiflora") Michaux (1964) found a separate procambium at the site of stamen initiation so early in floral development that only the sepal primordia were present. In other words, the double bundles are there first, before there are two appendages. We can assume that as the flower develops further these strands extend acropetally, retaining their duality, because that is the usual way with procambium.

The vascular diversity of *Ludwigia*'s locular planes contrasts strikingly with the uniformity of the septal planes. In sect. *Ludwigia*, sect. *Macrocarpon*, *L. foliobracteolata*, and *L. peruviana* bundles supplying style, stamens, and petals are discrete in the upper part of the ovary. In *L. hyssopifolia* and *L. latifolia* these bundles unite basally in the girdle and continue downward as one strand. In some other species the petal bundles end in the girdle while stamen or style bundles in the same planes pass by the girdle without merging. There are examples among the haplostemonous ludwigias (*L. abyssinica*, *L. epilobioides*, *L. prostrata*, and to some extent *L. torulosa*), as well as the diplostemonous ludwigias (sect. *Oligospermum*, sect. *Seminuda*, *L. densiflora*). In *L. linearis* and in the apetalous *L. ovalis*, bundles of the locular planes descend to a blind ending in the ovary wall. Most apetalous species have no bundles in the locular radii except the style bundles, these ending basally in the girdle. The diversity is linked in part to the presence or absence of petals and antepetalous stamens in the locular radii, in part to the thickness of the ovary wall. But these correlations do not explain every variant. In *L. arcuata*, for instance, complete bundles are wanting in some quadrants even though petals are present and the ovary wall is not especially thin. It occurred to me at one point that strong or weak development of bundles in the locular planes might be functionally based through a link with nectary size or stigma size, but a scanning of my serial sections turned up no such link. On the contrary, the stigma of *L. pilosa* is bigger than that of *L. alata*, though the latter is the one with complete bundles in the locular midplanes; and *L. alata*, *L. arcuata*, and *L. pilosa* all have well-developed nectaries while differing as to the development of the bundles in the locular midplanes.

Again, I think differences in developmental timing are important for explaining the vascular differences. Presumably, bundles develop along auxin gradients, the sources for the auxin often being a primordium at the distal pole and an already delineated but still differentiating vascular strand at the proximal pole. Ordinarily, the proximal pole is in an acropetally extending longitudinal strand. But in sect. *Oligospermum* and other taxa with the same peculiar petal supply we must assume the angle of the formative girdle is the proximal pole because that is where the midvein ends. The angle can be viewed as a sink getting auxin laterally from the two nearest sepal midveins along lines of intercellular stress. My reading of Michaux's (1964) research on *Ludwigia uruguayensis* suggests an explanation for the vascular difference between the several "peculiar" species and other lud-

wigias, namely, that the peculiar ones produce petal primordia out of the normal centripetal sequence—that is, after stamen primordia have been initiated and vascularized. Mayr's (1969) work showed that the initiation sequence can differ even between closely related species: the sequence is normal in *L. arcuata* but petals follow stamens in *L. repens* Forst. ("*L. natans* Ell."). Possibly the petal midveins of the peculiar species develop basipetally or bidirectionally. This must be true of at least some ludwigias; I do not know how else we would have species with the midveins running through the girdle to terminate blindly below it. In this connection it should be recalled that auxin usually moves basipetally. This is one reason why a pair of closely juxtaposed bundles can run the length of the ovary and not lose their duality; another is that an early action of auxin is to limit the number of cells programmed to divide and then differentiate (Sussex et al., 1972).

In *Ludwigia alata*, where there are bundles in the locular midplanes but no petal primordia to aid in their initiation, the distal auxin sources are probably the marginal meristems of the sepals. In other words, both the wings on the ovaries and the bundles in the wings reflect the strong lateral growth of the sepal primordia. Intensified lateral growth could result from selection pressure involving the persistent sepals as photosynthetic structures—for their ability to pay part of the energy cost of making seeds.

Differences in the way bundles of the locular midplanes interconnect do not help the taxonomist. Of course, the peculiarity in *Ludwigia peploides*—petal midveins ending in the girdle—is found in *L. uruguayensis*, a member of the same section. And the same peculiarity is shared by sect. *Seminuda* and *L. abyssinica*, where fruit structure (Eyde, 1978) indicates common ancestry. But differences between *Oligospermum* fruits and *Seminuda* fruits are so great that the vascular peculiarity must have arisen more than once within the genus. This seems remarkable in view of Sporne's (1976) survey of vascular girdles, for in a score of families with girdling bundles he found only one genus, *Viola*, with petal midveins ending in the girdle or, as he put it, "whose petals derive their entire vascular supply from that of the sepals." Among the onagrad, however, it turns out that the trait is not all that rare. Geerts (1909) and Kowalewicz (1956: 580) found, as I have, that the petal midveins of oenotheras end in the girdle. Fuchsias are variable for the trait. In *F. excorticata* (Forst.) L. f. and *F. paniculata* Lindl. the midveins end in the girdle; in *F. magellanica* Lam. they merge with the antepetalous stamen bundles in the girdle then continue basad as one bundle; and in some fuchsias there is no girdle (my observations). Unlike *Ludwigia*, *Fuchsia* and *Oenothera* have a floral tube above the ovary, and the explanation that I invoked for the vascular peculiarity—a difference in the timing of the initiation of floral appendages—runs into difficulty. To be sure, there are indications in the literature that onagrad with floral tubes differ developmentally among themselves as ludwigias do. Mayr (1969) found petal primordia and antesepalous stamen primordia arising simultaneously in a fuchsia; whereas Sattler (1973) found normal centripetal initiation of floral parts in another, and Hulbary & Nagaraja Rao (1959) reported the sequence to be sepals, carpels, stamens, petals in an oenothera. The difficulty for the timing explanation is that other oenotheras have normal centripetal initiation (Weisse, 1899; Pankow, 1966; Bunniger & Weberling, 1968; Mayr, 1969), yet as far as I know all have vascular peculiarities.

If there is a functional aspect to the termination of a petal midvein in the

girdle, it escapes me, but other bundles of the locular midplanes have at least one role besides transport. These bundles pass through the ovary wall in such a way as to help or hinder the eventual release of seeds. Geerts (1909: 121) pointed out that the position of the furrow along which each locule of an *Oenothera* capsule will split is established by a median vascular bundle supplying the antepetalous stamen; the bundle disappears, he said, as the fruit wall ripens. Comparable vascular strands in *Ludwigia*, on the other hand, can develop so as to retard dehiscence. The 1-seriate endocarp units of sect. *Oligospermum* are encaged by massive bundles, the one in each locular midplane fitting into a groove on the adaxial side of the endocarp. Much the same can be said of *Seminuda* fruits, though here the vascular structure is weaker. Apparently, fruits of both sections release seeds gradually and irregularly, even when wind-whipped or water-borne. Elsewhere in *Ludwigia* the link between vasculature and dehiscence is complicated by such factors as the shape of the fruit, the thickness of the wall between the bundles, and the strength of the septa. *Macrocarpon* fruits break up lengthwise along the furrows between the eight heavy bundles, and the seeds, being pluriseriate and smaller than those of *Oligospermum* and *Seminuda*, exit easily. Fruits of *L. palustris* can remain intact for months (Salisbury, 1972) even though the mid-locular segments of the fruit wall are paper-thin and devoid of a midvein (Eyde, 1978: fig. 10). In the lower, 1-seriate part of a *L. hyssopifolia* fruit the median bundles do not confine the endocarp units; instead they are deep enough to halve them, presumably providing for faster dispersal. In sect. *Ludwigia* the median bundles strengthen the "seedbox" that keeps the seeds from exiting laterally; evolution of this vascular trait may have provided the selection pressure that led to dehiscence through a terminal pore. Clearly, the genus *Ludwigia* would be a good subject for comparative research on dispersal.

Ludwigia's minor style bundles—style bundles in the septal planes—are a holdover, I think, from the ancestral condition. The presence or absence of these bundles does not simply reflect the size of the style base: style bases of *L. uruguayensis* are at least as big as those of its relative *L. peploides*, yet I found minor bundles well developed in the former, lacking in the latter. And *Hauya* styles, though bigger than those of any *Ludwigia* species, are vascularized only in the locular planes. Indeed, my survey of the family turned up no onagrads, *Ludwigia* aside, in which the style has septal vasculature. In the Melastomataceae the style can be vascularized in either way: some taxa have bundles in the locular planes only and others have them in the septal planes only (Eyde & Teeri, 1967; Subramanyam & Narayana, 1969). Some Myrtaceae have style bundles in both positions (see, for instance, Schmid, 1972a: fig. 30). This condition is probably ancestral because the others are readily derived from it and because it in turn is readily derived from an even older, distally apocarpous condition with three bundles per carpel.

Because of its taxonomic distribution, I judge that the central supply to the placentas is also a retained ancestral trait. I have not seen central bundles anywhere else in the Onagraceae except in *Epilobium nevadense* Munz (in only one of three microtomed flowers) and in one of the more specialized lopezias (Eyde & Morgan, 1973). In both of these instances the central supply must be considered either an anomaly or a phyletically secondary feature. In marked contrast, almost all *Ludwigia* species have a well-developed central system, and taxa with weakly

developed central bundles (*L. erecta*, sect. *Africana*, sect. *Macrocarpon*) are not among the most primitive ones with respect to other features. When I began this investigation I thought the central system must be ontogenetically secondary—made up of late-developing, anastomosing branches from the transseptal bundles. I dropped this notion after I sectioned buds with the floral vascular system at an early stage and found procambium for central bundles already linked to the big outer strands at the flower's base. Now I view the central supply as one mark of *Ludwigia*'s early evolutionary divergence from the ancestral Onagraceae. The myrtalean precursors must have had a central supply to the placentas in common with other syncarpous angiosperms, and the trait has been retained in most modern Myrtales. It disappeared from the main onagraceous line and stayed on with the newly evolving transseptal system only in the line that led to *Ludwigia*. Why did *Ludwigia* alone keep the dual supply? Recall that many of its species, among them the woodier ludwigias of the tropics, have the most deeply intrusive, highly ovuliferous placentas in the family. Natural selection favored the two-way system because reduction to a single set of bundles would have meant smaller placentas, fewer ovules, and a commensurate drop in reproductive success.

Transseptal bundles no longer seem as peculiar as they once did (Eyde, 1967). In recent years species with all or part of the ovular supply crossing the septa have been found in several families, especially in families with inferior ovaries. The list includes Caprifoliaceae (Fukuoka, 1973), Lecythidaceae (Monteiro-Scanavacca, 1974, 1975), Myrtaceae (Schmid, 1972b: 433), Oliniaceae (Rao & Dahlgren, 1969), Rubiaceae (Rao et al., 1964), and Trapaceae (Orchard, 1975). Lecythidaceae, Myrtaceae, Oliniaceae, Onagraceae, and Trapaceae are all myrtalean in one treatment or another (see Briggs & Johnson, 1979: 160), but their transseptal bundles can not be taken as proof of close common ancestry because it is clear that transseptal bundles have evolved repeatedly. Schmid's work with *Eugenia* and *Syzygium*, for example, indicates that the transseptal supply evolved independently in the ancestors of *Eugenia* s. str., though the trait is common elsewhere in subfamily Myrtoideae. And I have learned from conversations with Rubiaceae specialist J. Kirkbride that the rubiads with transseptal bundles are a mixed lot, unrelated by other structural features.

If transseptal vasculature evolved more than once in the Myrtaceae and in the Rubiaceae, it could have evolved more than once in the Onagraceae. I think it did. That is, I infer that *Ludwigia*'s ancestors and the common ancestors of all other Onagraceae developed the trait separately after they diverged. The inference accords with the observation that only *Ludwigia* regularly has both a central system and a transseptal system. It also accords with an idea I shall put forward in subsequent paragraphs, namely, that the inferior ovary evolved independently in *Ludwigia*. It will be seen that an independently evolved inferior ovary accounts for *Ludwigia*'s lack of a floral tube and for the puzzling position of *Ludwigia*'s nectaries.

LUDWIGIA'S NECTARIES EXPLAINED

Sunken, hair-rimmed nectaries are ancestral in *Ludwigia*. The way in which they are associated with diplostemony and with other ancestral features makes this clear. But these sunken nectaries—indeed all *Ludwigia* nectaries, sunken or

raised—are on the ovary's summit. No other onagrads have nectaries on the gynoecium. Most have them at the base of a floral tube, and the nectariferous tissue is then seen in sectioned material as part of the floral tube because it is on the outer side of the notch where the tube merges with the gynoecium. A few of the onagrads—aside from *Ludwigia*—are tubeless or almost so: *Gayophytum*, *Gongylocarpus*, species of *Circaea*, *Epilobium*, and *Lopezia*. Here again, the nectaries are on the appendage side of the appendage-gynoecium junction. In *Gayophytum*, *Gongylocarpus*, and some *circaeas* cross-sections through the junction show the base of the slender style encircled by the nectary in such a way that an ancestral tube is easily envisioned (Fig. 21). The *epilobiums* with free perianth parts above the ovary (sect. *Chamaenerion*) have their stamens united basally in a short stamen tube, and the nectariferous tissue is on the inner side of this tube (Mikhailova, 1964; Kartashova, 1965). Nectaries are also androecial in the tubeless species of *Lopezia*. I once thought *Ludwigia*'s nectaries more akin to *Lopezia*'s than to other onagraceous nectaries (Eyde & Morgan, 1973) but that idea led nowhere, and knowing *Ludwigia* better I have given it up.

How is an evolutionary anatomist to explain the aberrant position of *Ludwigia*'s nectaries? Surely a structure so important for the plant's reproductive success does not move about capriciously in the course of evolution or disappear and reevolve in a different place. The answer, I think, is that nectary position diverged while the ovaries were superior. I envision proto-Onagraceae in which the ovaries stood free within a floral cup, a condition that is retained in the related family Lythraceae. These precursors probably had secretory tissue lining the cup-gynoecium junction, with the tissue more to one side of the junction or the other, depending on the species, for that is just what is found in modern Lythraceae. In *Decodon verticillatus* (L.) Ell., for instance, the nectariferous tissue is unmistakably gynoecial, rising up the ovary to a level above the locule bases (flowers from Anne Arundel County, Maryland, no voucher). *Ammannia coccinea* Rottb., on the other hand, shows a small nectary slightly to the cup side of the junction (Smith & Herr, 1971: fig. 1), and the bat-pollinated flower of *Lafoensia pacari* St. Hil. has a big nectary mostly on the cup side of the junction (Sazima & Sazima, 1975: fig. 3). My sections of *Lythrum salicaria* L. (garden flowers, no voucher) show nectariferous tissue lining the junction and extending up both sides about equally. I have seen densely staining tissue similarly placed in flowers from garden plantings of *Lagerstroemia indica* L.—though as far as I know *lagerstroemias* no longer secrete nectar—and Mahabale & Deshpande (1957: fig. 30) show a differentiated region extending deep below the cup-gynoecium junction in the lythraceous shrub *Woodfordia*. I think this junction, the notch between gynoecium and surrounding parts, is the ancestral site of nectar secretion for the Myrtales and for many other dicots. From this position, the nectary could extend phyletically up one side or the other; either way would increase the secretory surface. But secondary phyletic migration of the nectary from the outer side and across the junction to the inner side, or vice versa, would likely require more mutations than the initial shift, and would therefore be a less frequent evolutionary event.

The idea that nectaries do not easily pass from one side of the junction to the other is not altogether new. Feldhofen's (1933) survey named several families of dicots in which the floral nectaries are constant in form and position. And Brown's

classic attempt to look at nectaries phyletically postulated two lineages originating in the Theales, one with gynoecial nectaries, the other, including the Caryophyllales and allies, with androecial nectaries (Brown, 1938: 555–556). Although many of Brown's views now seem oversimple, Zandonella's (1972, 1977) thorough investigation of the Caryophyllales sustains Brown's opinion on that group (see also Rohweder & Huber, 1974: 343). Androecial nectaries are indeed a constant feature of the alliance except in the primitive family Phytolaccaceae, where the nectary is between the androecium and the ovary, presumably in the ancestral position. The Caryophyllales are particularly effective for showing constancy of nectary position because flowers of the constituent families have been modified in so many ways. The ovary has become inferior in the Aizoaceae, for example, without shifting the nectary away from the androecial side of the junction. Outside this alliance there are groups in which all members have gynoecial nectaries. In the Gesneriaceae (Wilson, 1974a, 1974b; Skog, 1976) the nectary develops as an annular outgrowth from the very base of a superior gynoecium or as a histologically differentiated region of the ovary wall. The only ambiguity is in the tribe Gesnerieae. Here the nectariferous tissue emerges from the junction where the epigynous part of the flower meets the inferior or partly inferior ovary; it is neither more to the gynoecial side nor more to the androecial side. In the Acanthaceae and the Scrophulariaceae, families close to the Gesneriaceae, nectaries are likewise located at the junction or to the gynoecial side (Feldhofen, 1933: 595; Cosa, 1975). The same is true, I think, of the Crassulaceae and the Ericaceae. In the Rosaceae, on the other hand, the nectary is always part of the floral cup; that is, it is on the androecial side of the junction.

Admittedly, there are a few families in which evolutionary processes probably moved the nectary across the junction. In most Myrtaceae the nectary is on a floral tube or cup (see Kartashova, 1965: 162; Dawson, 1970: 433; Carr et al., 1970)—a sign, perhaps, of common ancestry with the Rosaceae—but sectioned flowers of *Rhodomyrtus tomentosa* (Aiton) Hassk. (from two herbarium collections and from plants cultivated in Florida) show dense tissue that I take to be nectariferous on the summit of the inferior ovary. And R. Schmid tells me the *Syzygium* nectary can be at the junction, on the androecial side of the junction, or on the gynoecial side, depending on the species. I infer that the gynoecial nectary is derived in the Myrtaceae, having migrated phyletically from the floral cup. (As far as I know, there are no gynoecial nectaries among the myrtads with superior ovaries, and these should be closest to the family's ancestry.) Caprifoliaceae is another family with nectaries on both sides of the junction. They are on top of the inferior ovary in *Sambucus* and *Viburnum*, on an epigynous tube in other genera. Some years ago this heterogeneity could have been discounted on the grounds that *Sambucus* and *Viburnum* do not really belong to the Caprifoliaceae, but recent phytochemical work seems to make them bona fide caprifoliads (Bohm & Glennie, 1971; Boulter et al., 1979). If the family is monophyletic, it is likely that the nectary has crossed the junction in one direction or the other. Most Rubiaceae have the nectary on top of an inferior ovary, but a few genera—*Cephalanthus* and *Uncaria* are examples—have the nectary on the androecial side. This does not upset my argument, for I think all such nectaries belong to rubiads with capitate inflorescences, where the flowers have been squeezed, so to speak, into a more slender form. In some of these capitate taxa a little meri-

stematic activity has evolved beneath the nectary, raising it a bit, making it part of the tube, and thereby reducing the flower's girth. The required structural change is slight. More troublesome to me is *Mastixiodendron*, a rubiaceous genus that has no tube, the stamens and petals diverging individually from the gynoecium. I say the genus is troublesome because it is believed that *Mastixiodendron*'s ancestors had a floral tube (Darwin, 1977), because the *Mastixiodendron* ovary, like that of *Ludwigia*, can be partly superior, because I judge from the appearance of microtomed herbarium flowers—*M. pachyclados* (K. Schum.) Melch., NGF 17392—that the superior part of the ovary is nectariferous, and because a critic familiar with *Mastixiodendron* could weigh all this and draw a false parallel with *Ludwigia*.

If it can be inferred that *Mastixiodendron* has lost its tube, why should we not think the same of *Ludwigia*? One reason is that *Mastixiodendron* is not as isolated from other Rubiaceae as *Ludwigia* is from other Onagraceae. Indeed, *Mastixiodendron* seems to be a good member of the Chiococceae, a tribe in which other genera show a diminution of the floral tube in varying degree (Darwin, 1977). A more compelling reason for looking at *Ludwigia* differently is the independent evidence—evidence of at least four kinds—that *Ludwigia* is an early evolutionary offshoot. I discussed *Ludwigia*'s 4+-merism in a previous account (Eyde, 1977) and its central vascular system earlier in this article. To these lines of evidence may be added the evidence of flavonoid chemistry and of pollen morphology. J. Averett and P. Raven tell me their initial analyses show an archaic distribution of flavonols and glycoflavones in *Ludwigia* to match the other signs that it is an early offshoot. And *Ludwigia*'s pollen grains have the simple, smooth viscin threads thought to be ancestral for the family (Skvarla et al., 1978). *Ludwigia* species are unspecialized with regard to pollination: they have generalized flowers pollinated by generalized insects (see Estes & Thorp, 1974). If *Ludwigia* diverged from the other onagrads while the ovary was superior, it need never have been pollinated by anything but insect generalists, and it need never have had much of a floral tube—just a modest cup in keeping with its myrtalean ancestry and that disappearing as the ovary became inferior. Indeed, the making of a floral cup would be wasteful if the ciliated depressions on the gynoecium secrete and hold enough nectar to ensure pollination.

The realization that *Ludwigia* need never have had a floral tube beyond the ovary is a turnabout. Before I began to work on this article I thought all present-day onagrads had ancestors with floral tubes. This in turn implied that the ancestors of all present-day onagrads had coevolved with hummingbirds, an implication at odds with the fossil record because onagraceous remains can be found from the Lower Paleocene onward, whereas there were no hummingbirds, it is thought, until the Eocene Epoch or later (Sussman & Raven, 1978). The record seemed to require "an extinct group of insect-pollinated Onagraceae, older than all bird-pollinated Onagraceae" (Eyde & Morgan, 1973: 785–786). Though that requirement is met in principle by my new interpretation, the old insect-pollinated Onagraceae are not all extinct: *Ludwigia* survives.

DIAGRAMMING THE DUBIOSITIES

Figure 22 is meant to show some of the changes that took place as *Ludwigia* diversified. It combines my thoughts on *Ludwigia*'s evolution with those of Raven

and his coworkers (Raven, 1963, 1980; Skvarla et al., 1978; Ramamoorthy, 1979; Raven & Tai, 1979). Some parts of the diagram are more speculative than others. For example, the placing of *L. hyssopifolia* is somewhat arbitrary, whereas the central position of the *Myrtocarpus* complex is well founded. Relative size of the lobes roughly reflects the number of species surviving in the corresponding taxa, but the distance between points on the diagram is not supposed to suggest relative lapse of time between evolutionary changes. The diagrammatic derivation of one group from another should not be taken too literally. Deriving sect. *Ludwigia* from the *Myrtocarpus* complex does not mean the ancestors are among the extant species. It means I have in mind forebears that would fit fairly well into the *Myrtocarpus* complex if we could recall them from the past.

“*Myrtocarpus* complex” is my term of convenience encompassing sect. *Myrtocarpus* s. str. and two related sections, *Michelia* and *Pterocaulon*. In this complex and nowhere else in *Ludwigia* are found woody perennials with diplostemonous flowers—some of them 4+-merous—and relatively unspecialized fruits. The ovaries often have high summits and longitudinal sections show they can be slightly superior (see pls. 28, 30 in Micheli, 1875). Structurally most primitive within the complex are shrubby, outcrossing perennials of sects. *Michelia* and *Myrtocarpus*. Except for *L. nervosa* (Poir.) Hara, however, these species are polyploids (Ramamoorthy, pers. comm.). *Pterocaulon* species retain the diploid number but stand apart in that they are self-compatible, predominantly inbreeding annual herbs with 4-merous flowers. Ancestral members of the complex must have had the diploidy of this section joined with the 4+-mery and woody habit now largely restricted to sects. *Michelia* and *Myrtocarpus* s. str. Thus the *Myrtocarpus* complex—and the genus as a whole—exemplify a generalization drawn from chromosome numbers in the Winteraceae and other archaic angiosperms: polyploidy can buffer against divergence and paleopolyploids therefore tend to preserve more primitive characters than diploids or low polyploids that have diverged more actively (Ehrendorfer et al., 1968: 349; see also Stebbins, 1980).

Sect. *Oligospermum* diverges first for several reasons. One is that *Oligospermum* fruits lack the spongy layer common among diplostemonous ludwigias, and I think they always did (Eyde, 1978). Diploidy, 5(6)-mery, and well-developed minor style bundles are other signs of antiquity. With *Oligospermum* in this position, the evolution of its 1-seriate ovules and herbaceous habit must be seen as independent events—independent of their evolution elsewhere in the genus—and *Oligospermum*'s solitary pollen grains can be primitively so, predating the tetrads and polyads of sect. *Seminuda* and the *Myrtocarpus* complex. I say *Oligospermum*'s pollen monads can be primitive because that would link the *Ludwigia* lineage palynologically with the main onagraceous line, in which monads are undoubtedly primitive. When I look at *Ludwigia*'s flowers functionally, however, I see a nice counterargument. If intrusive placentas and a dual ovular supply are among the earliest specialized features of the *Ludwigia* line, the selective pressure for the divergence of that line must have been increasing the number of ovules per flower. *Ludwigia*'s precursors, the ancestors of all onagrads, had already increased pollination efficiency by evolving viscin threads (Cruden & Jensen, 1979). What would better complete the evolutionary package for the early ludwigias than an early changeover from pollen monads to tetrads

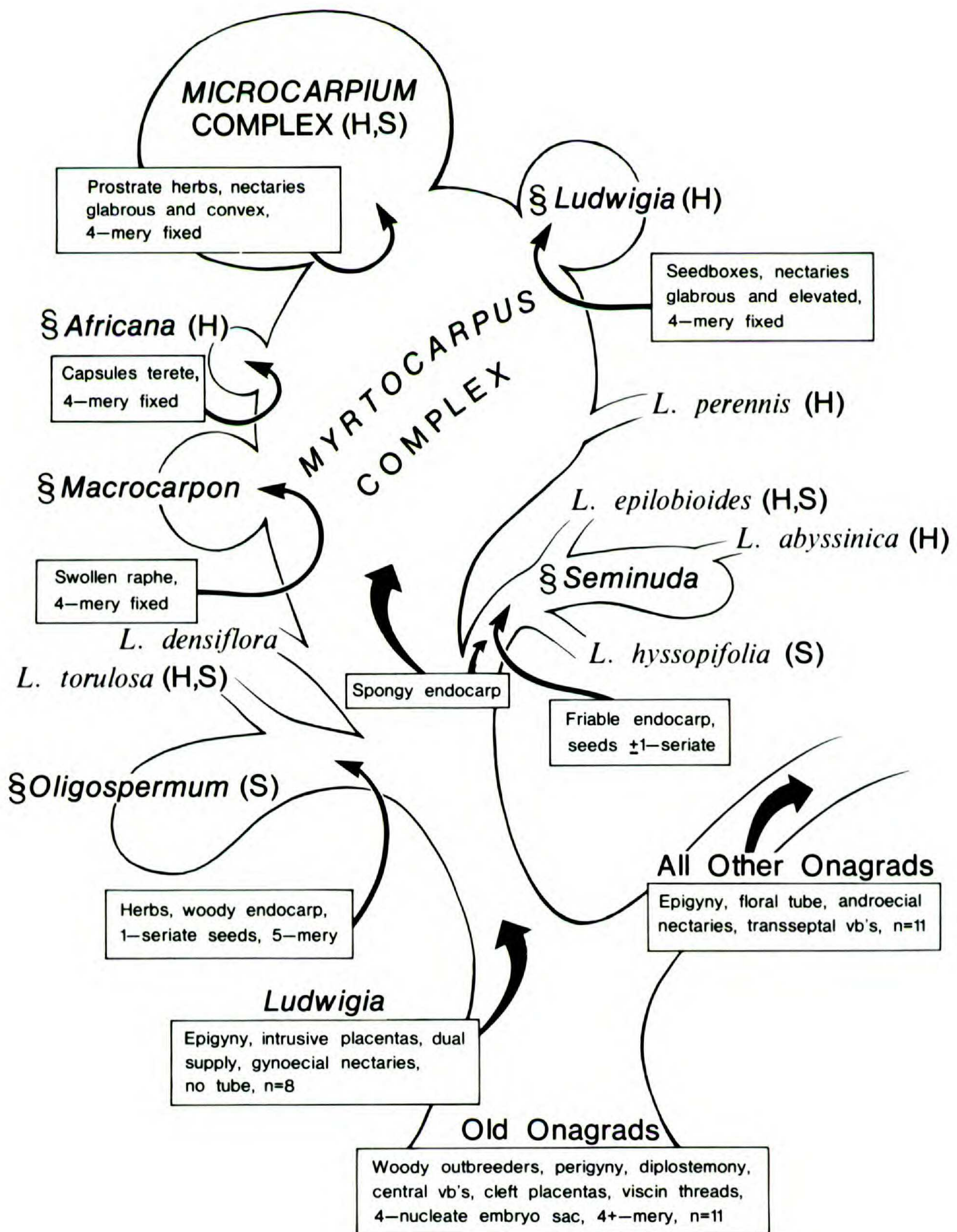


FIGURE 22. Evolution in *Ludwigia*. Some infrageneric sections are left out and some ideas are founded more firmly than others; for details see text of this article and its two forerunners. The gametic chromosome numbers 8 and 11 are ancestral; many Onagraceae now have derived numbers. (S) marks species in which all pollen is shed as monads and groups in which some species (*Microcarpium* complex) or all species (sect. *Oligospermum*) shed only monads. (H) marks taxa that are at least partly haplostemonous. The *Myrtocarpus* complex is treated as wholly diplostemonous, though one species, *L. inclinata*, has some haplostemonous populations.

and polyads? In an outcrossing population, this would provide for the fertilization of more ovules while not requiring that the number of insect visits be increased. Evolution is thought to have taken this course without viscin threads in the Annonaceae and some other families (Walker, 1971: 43). If *Ludwigia*'s early evolution involved a functional linking of pollen tetrads with intrusive placentas and dual ovular supply, we can infer from *Oligospermum*'s retention of the dual supply that monads were abandoned before *Oligospermum* diverged. After *Ludwigia* had diversified further, its subdivisions adopting a variety of dispersal strategies, descendants with reduced placentas could revert to monads without disadvantage and some did.

The ancestors of *Ludwigia torulosa*, a 5-merous, haplostemonous species with *Oligospermum*-like endocarps, would probably fit well in *Oligospermum* as the diagram indicates. Ovaries of sect. *Seminuda* have a spongy zone like the ovaries of present-day members of the *Myrtocarpus* complex. The diagram gives this feature a single origin preceding the divergence of *Seminuda* but following the divergence of *Oligospermum*. All ludwigias up to this level are 4+-merous and diploid. Although surviving *Seminuda* species are polyploid with 1-seriate seeds, ancestral diploids in the lineage may have given rise to *L. hyssopifolia*, a 4-merous species with upper seeds pluriseriate, before 1-seriate seeds became a fixed feature. *Ludwigia epilobioides*, often 4+-merous and with imperfectly 1-seriate seeds, could have a similar origin, but the branching off of this species from the *Seminuda* line would have involved androecial reduction and an increase in chromosome number, *L. epilobioides* being haplostemonous and hexaploid. *Ludwigia hyssopifolia* and *L. epilobioides* could be placed differently in the diagram. One could, for example, attribute primitiveness to their solitary pollen grains (*Seminuda* pollen is in tetrads) and argue that each acquired its fruit and seed characters independently of the other and of the *Seminuda* line. The way I place them is simplest because friable ("corky") endocarp tissue is made to evolve only once, but I am not at all sure that is the way it was (Eyde, 1978: 674). The position of *L. abyssinica* is less doubtful. In all respects it looks like a haplostemonous derivative of sect. *Seminuda*.

In making *Ludwigia densiflora* an offshoot from the ancestral members of the *Myrtocarpus* complex, I have in mind that it retains at least two of *Ludwigia*'s old traits, diploidy and 4+-mery. The *L. densiflora* ovary has no spongy layer. I guessed in an earlier article that the spongy character has been lost, but the ovary could be primitively without a spongy layer if the forerunners of this aberrant species branched off early enough. *Ludwigia latifolia*, not included in the diagram, would be made a more recent offshoot from the *Myrtocarpus* complex. Like *L. densiflora*, it lacks a spongy layer. Here I judge the likelihood greater that the spongy layer has been lost because *L. latifolia* seems much closer than *L. densiflora* to extant *Myrtocarpus* species.

Macrocarpon is made a fairly early-diverging section despite its advanced features—4-mery and the peculiar swollen raphes on its seeds—for it is an outbreeding group with some diploidy in it that stems from old, long-departed diploids, not from modern sect. *Pterocaulon*. Floral vascular bundles are separate to an unexpected degree in *Macrocarpon*, a point of similarity with *Ludwigia peruviana* and *L. foliobracteolata* in *Myrtocarpus* s. str. In addition, there are

fossils to suggest that *Macrocarpon* species are not neophytes. *Ludwigia* seeds with big raphes have been found in the Middle Miocene FASTERHOLT brown coal of Jutland (Friis, 1980). Though *Macrocarpon* is mostly tropical, it would not be altogether out of place in the Danish Miocene: as a whole the FASTERHOLT assemblage is like the present flora of our southeastern states (Friis, 1975), at the northern end of the *Macrocarpon* range.

The diagram makes the origins of sect. *Ludwigia* and the *Microcarpium* complex (sects. *Dantia*, *Microcarpium*, and *Miquelia*) more recent than that of sect. *Macrocarpon*. Actually, one can say for sure only that, as regards such traits as haplostemony and modified nectaries, these groups are more highly evolved than *Macrocarpon*. Hybridization experiments confirm the genetic affinity of the three sections of the *Microcarpium* complex (Peng Ching-I, unpubl.), and a common origin near sect. *Pterocaulon* seems possible. Crosses have also been tried between members of sect. *Ludwigia* and members of the *Microcarpium* complex, and seed set has followed some of these attempts (P. Raven, pers. comm.). But seed set alone can not be taken as proof of close kinship because *Ludwigia* may be a genus in which seeds can result from remote crosses: reportedly, seeds have developed from the crossing of *L. leptocarpa*, in sect. *Seminuda*, with *L. octovalvis*, in sect. *Macrocarpon* (Ormond, 1973; attempts to duplicate this at the Missouri Botanical Garden have failed). Furthermore, structural features seem to make the bond between the *Myrtocarpus* complex and sect. *Ludwigia* tighter than the bond between the *Myrtocarpus* and *Microcarpium* complexes. The dehiscence pore in a fruit of sect. *Ludwigia* is much like the comparable region of *L. peruviana* or one of its allies (Eyde, 1978: figs. 7, 8). And the nectary of sect. *Ludwigia*, though hairless, is like a *Myrtocarpus* nectary in that it is more or less upright and can be at least slightly depressed. If we read these resemblances as signs of kinship, we may then ask whether sect. *Ludwigia* was an offshoot from the line that led to the *Microcarpium* complex and whether sect. *Ludwigia*'s nectary shows a stage in the evolution of the *Microcarpium* nectary. I think not; that is, I judge that the two groups differ enough to have arisen independently from the *Myrtocarpus* complex. But the judgment is based on weaker evidence than one would like. A clearer understanding of the evolution of glabrous nectaries from hairy ones would help. The only thing clear about that now is that it happened more than once.

The nectaries of *Ludwigia perennis*, for example, are like those of sect. *Ludwigia*, but the similarity doubtless results from parallel evolution, for *L. perennis*'s fruits are not at all like sect. *Ludwigia*'s seedboxes. The placing of *L. perennis*—and of sect. *Africana*—relative to other taxa is arbitrary. Both probably originated from the *Myrtocarpus* complex, but floral structure offers no clues beyond that. The position of *L. prostrata*, not diagrammed, is even more uncertain. Emphasizing the absence of major style bundles in the locular radii (of the one collection that I looked at!) would make it the only survivor of a very early-diverging line. Stressing the more or less 1-seriate seeds would make it an offshoot of the *Seminuda* line. Or perhaps it is still another specialized descendant of the old diploids of the *Myrtocarpus* complex.

I picture the ancestral *Ludwigia* flower with little or no floral cup and the ovary only partly inferior, but with placentas already deeply intrusive and many-

ovuled. Still older ancestors, common to all Onagraceae, had superior ovaries; they also had cleft placentas with ovules roughly 2-ranked as in modern *Hauya* and some fuchsias. The styles had bundles in both the septal radii and the locular radii. Sepals, petals, and stamens ended basally in a floral cup and nectaries were at the junction where the cup met the base of the gynoecium. These proto-onagrads lacked the inferior ovary, one of the traits by which the modern Onagraceae are separated from, say, the Lythraceae; however, we can assume they had already acquired onagraceous pollen features, the onagraceous embryo sac, and diplostemony because those traits are found in both the *Ludwigia* line and the main onagraceous line. Flowers became epigynous in each of these daughter lines after they diverged, and in the *Ludwigia* line the nectaries shifted to the gynoecium while the floral cup, its adaptive value diminishing as gynoecial nectaries improved, was lost. An earlier diagram by Broekens (1924: 487) agrees with mine as to the antiquity of *Ludwigia*. But *Ludwigia* ("Jussieua") is not, as Broekens thought, the *Stammvater* of the other Onagraceae. It is the *Stammschwester*.

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